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This Journal, which was founded in 1913 as the organ of The British Ecological Society, was the first periodical devoted exclusively to ecology. It contains original contributions to general and plant ecology, *The Biological Flora of the British Isles*, reviews, and reports of the meetings of the British Ecological Society.

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BLACKWELL SCIENTIFIC PUBLICATIONS

A FURTHER STUDY OF THE ZINC-POLLUTED RIVER YSTWYTH

By J. R. ERICHSEN JONES

Department of Zoology, University College of Wales, Aberystwyth

(With 4 Figures in the Text)

One of the outstanding features of pollution by heavy metals is its persistence. A river polluted by organic matter can recover lower down its course when the offending substances have been oxidized but once soluble salts of lead, zinc or copper find their way into a river no natural agency can remove them, though dilution by unpolluted tributaries can lessen their concentration. Metallic pollution can be very persistent in time and the river Ystwyth in north Cardiganshire is an interesting example for it remains seriously polluted by zinc thirty-five years after the cessation of mining activities in its valley. The first scientific examination of the main stream was made by Carpenter (1924) who found that the fauna seemed limited to nine species, all belonging to the animal groups Insecta, Hydracarina and Crustacea-Entomostraca. The flora was also very poor, the only common algae being *Batrachospermum* and *Lemanea* (*Saccheria*). This was attributed to pollution by lead salts, and analyses made in 1921-22 showed that the river carried 0·4-0·5 mg/l. of lead in solution (Carpenter 1924, p. 12). The presence of zinc was not suspected at this time, though it was well known that the Ystwyth mines yielded lead, zinc and silver ores and no tests for zinc were made. In 1939-40 the writer (Jones 1940) made a study of the river which proved to be polluted by lead and zinc, the former in concentrations up to 0·05 mg/l., the latter in concentrations of 0·2-1·2 mg/l. It was shown that the main sources of pollution were the Cwm Ystwyth, Frongoch and Wemyss mines and a brief description was given of the river's fauna and flora.

The present paper carries the investigation some stages further; it includes a resurvey of the sources of pollution, further observations on the flora and the chemical condition of the main stream, the results of quantitative sampling of the fauna and an account of the feeding habits of the chief insect species.

THE FLORA OF THE MAIN STREAM AND THE SOURCES OF POLLUTION

The topography of the river has been described in my previous paper. It rises on the Plynlimon plateau about 18 miles from Aberystwyth (Fig. 1) and in its upper reaches is a fine mountain stream with a good flow of water and a stable bed mainly composed of large, flattened stones and boulders with occasional stretches of rock. Trout are plentiful and the flora of the stream-bed is luxuriant. The moss *Fontinalis antipyretica* L. is common and on many stones there is a heavy growth of *Lemanea*

mammillosa Kütz. In a dry, sunny spring the whole of the stream-bed not covered by these plants will develop a thick mat of green-brown growth. *Stigeoclonium* is the dominant green alga, mixed with this is a little *Zygnaema*, *Mougeotia* and *Spirogyra*; *Tabellaria flocculosa* and *Ceratoneis arcus* are the dominant diatoms, other diatoms collected are listed in Table 1.

About 7 miles from its source the river flows past the Cwm Ystwyth mine and it is here that it begins to be polluted. An assemblage of ruined buildings, heaps of broken rock and dumps of mine-refuse lies on the right side of the valley (Fig. 2). The results of a series of determinations of the zinc concentration of the main stream are inserted in Fig. 2 and show how the zinc content mounts as the river

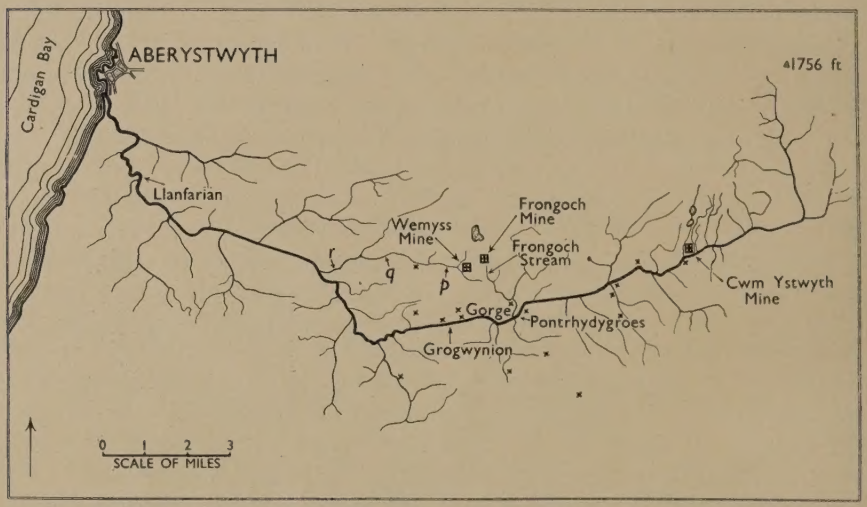

Fig. 1. Map of the river Ystwyth showing the positions of the localities mentioned in the text. Lead mines which are sources of pollution are indicated by large squares; other mines are indicated by crosses. Fauna samples were taken at Llanfarian. Water samples for analysis were taken at the Cwm Ystwyth mine (for details see Fig. 2 and Table 2), from the Frongoch stream at the point indicated by the arrow, at Grogwynion and Llanfarian, and from the stream draining the dumps of the Wemyss mine at *p*, *q* and *r*.

passes the derelict mine. In my earlier study it was shown that the chief sources of pollution are three adit effluents (Fig. 2, *a*, *b* and *d*). In 1939 all three were heavily polluted with zinc and one (*a*) heavily polluted with lead. New analyses of these adit effluents made in 1953 and 1956 (Table 2) show no measurable amount of lead but zinc is still present though in reduced concentrations. This, of course, may be compensated by changes in their rate of flow. Adit effluent *a* seems to be the most important individual source of pollution at the Cwm Ystwyth mine, being greater in volume and more constant in discharge than the others. It is reputed to be the overflow of water accumulating in one of the largest and most recently worked shafts. Effluent *b* was dry on 11 June 1953 but on 27 October and 3 November 1956 had a good flow of water. Effluent *d* is now a very small trickle 9-10 in. wide and

about 2 in. deep. The other streams running over the dumps were all tested on 3 November 1956 but none showed any appreciable degree of pollution; in the course of time these streams, which plunge down from the escarpment above, seem to have carried away all the fine material in their course and now run over beds of rough, broken rock.

Zinc concentrations above 1 mg/l. were measured by the turbidimetric method described in *Approved Methods for the Physical and Chemical Examination of Water* (Anon. 1949), the samples being diluted with distilled water as necessary. Tests for lead and iron were made as described in the same paper. Sulphate estimations are gravimetric and chloride measured by titration with silver nitrate. Zinc concentrations less than 1 mg/l. are turbidimetric estimations using sodium diethyldithiocarbamate. This reagent gives a perceptible turbidity with zinc down to 0·1 mg/l. and with practice and in the absence of iron and copper reasonably accurate estimations can be made using 0·1-1·0 mg/l. standards in Nessler cylinders.

Table 1. *The diatoms of the upper reaches of the river Ystwyth*

This list is based on samples taken from the main stream above the Cwm Ystwyth mine in May and June 1953. The nomenclature is that of Hustedt (1930).

1. Dominant species
   - *Tabellaria flocculosa* (Roth) Kütz.
   - *Ceratoneis arcus* Kütz. and varieties

2. Sub-dominants
   - *Fragilaria capucina* Desmaz.
   - *Achnanthes minutissima* Kütz. var. *cryptocephala* Grun.
   - *Gomphonema parvulum* (Kütz.) Grun.

3. Common
   - *Frustulia rhomboides* (Ehr.) de Toni
   - *Stauroneis phoenicenteron* Ehr.
   - *Cymbella gracilis* (Rabh.) Cleve
   - *Gomphonema acuminatum* Ehr.
   - *G. constrictum* Ehr.
   - *Surirella linearis* W. Smith

4. Rare
   - *Meridion circulare* Ag.
   - *Diatoma vulgare* var. *mesodon* (Ehr.) Grun.
   - *Fragilaria intermedia* Grun.
   - *Eunotia robusta* var. *tetraodon* (Ehr.) Ralfs
   - *Achnanthes lanceolata* Bréb.
   - *Frustulia vulgaria* Thwaites
   - *Navicula viridula* Kütz.
   - *Pinnularia interrupta* W. Smith
   - *P. borealis* Ehr.

Immediately below the mine the flora is not greatly changed but at Pontrhydygroes the whole appearance of the river has altered. The moss and the rich, growth of green algae and diatoms have disappeared; the *Lemanea*, however, is abundant and most of the stream-bed, at some points, is covered with this alga. Below Pontrhydygroes bridge the Frongoch stream flows into the river; this has its source at the Frongoch mine about 1½ miles to the N.W. A sample taken near the mine in 1939 contained 57 mg/l. of zinc and 3 mg/l. of lead. New analyses of samples taken at the same spot in 1953 and 1956 are given in Table 2 and show that 40-90 mg/l. of zinc is present but that the lead has almost disappeared. On a number of occasions attempts were made to measure the flow of the stream at the point where the samples were taken, by running in 2-3 litres of dyed water at a constant, known discharge rate (1200 ml/min), taking samples lower down the channel and measuring the dilution colorimetrically. The results are given in Table 2 but

the method did not prove very satisfactory as the flow of the stream is very irregular, particularly at low level and mixing did not seem to be perfectly even. Aniline blue and safranin were found to be satisfactory dyes. The discharge of effluents *a* and *b* at Cwm Ystwyth was measured in the same way and here the results were much more satisfactory as the dye solution mixed evenly with the stream water.

Below the Frongoch stream the river enters a short gorge and when it emerges its character is greatly changed. The stream-bed is silted up and very unstable, a monotonous expanse of weathered pebbles and gravel over which the stream

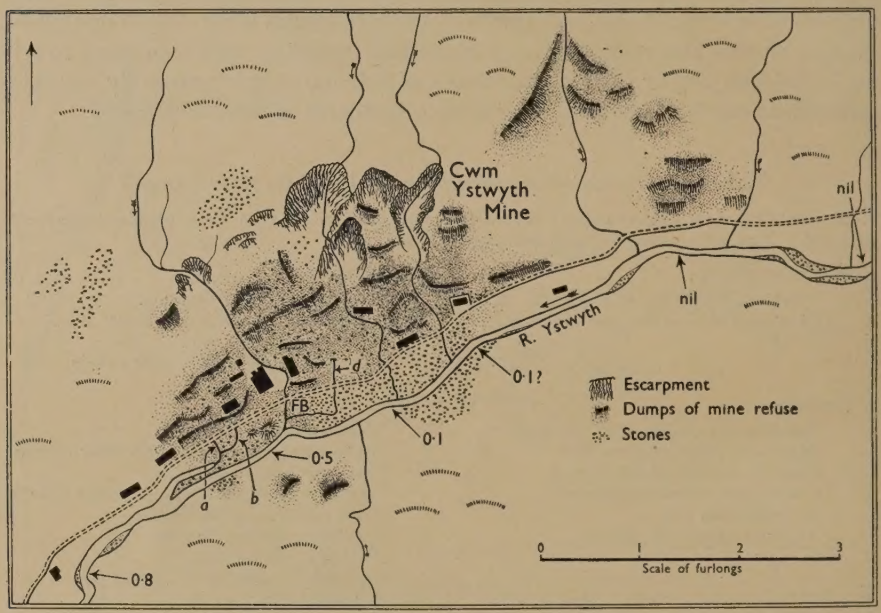

Fig. 2. The Cwm Ystwyth mine. *a*, *b* and *d* are the adit effluents for which analyses are given in Table 2. The arrows and figures along the main stream of the river are the results (mg Zn/litre) of a series of analyses made on 27 October 1956; the sharp rise from 0·1 to 0·5 appeared to be associated with a copious seepage of water from the old filter beds, FB.

meanders. The flora is very poor, the *Lemanea* has disappeared except at a few points where big stones are firmly lodged in deep water. Flattened stones in shallow water bear patches of algae of the *Chamaesiphon* type and from time to time a thin growth of encrusting algae and diatoms may develop but for the most part the stream-bed seems barren. With little or no improvement the river continues its way to the sea. Nearer Aberystwyth it is more confined by high banks and its rubble flood beaches are of normal size. Its tributaries are not numerous and all are short so that the volume of water carried at Aberystwyth does not greatly exceed that at the Cwm Ystwyth mine. On 8 June 1953 when the level of the river was about normal, cross-sections of representative parts of the main stream

at Llanfarian were measured. A moderately fast section chosen was 33 ft in width and had an average depth of 6½ in. (approximately 18 sq. ft). A typical slack section measured 48 ft across and had an average depth of 8 in. (32 sq. ft). A series of measurements of the surface current across the fast section gave an average value of 2 ft/sec. The mean current through the whole cross-section can be taken as 0·8 times the mean surface current when the river bed is composed of coarse materials (Welch 1948, pp. 153-4). This gives a discharge rate for the main

Table 2. *Analytical data for the main stream at Llanfarian and for the various sources of pollution*

The discharge for the effluent streams is given in litres/min. Concentrations of Zn, SO_4, Pb and Cl are mg/litre. tr., trace; nd, not detected. A dash implies no determination. For locations of samples see Figs. 1 and 2.

	pH	Zn	SO_4	Fe	Pb	Cl	Discharge
LLANFARIAN							
3 June 1953	–	0·6	5	nd	<0·1	9·6	–
27 May 1956	6·8	0·5	5	–	–	–	–
3 November 1956	6·8	0·6	–	tr.	–	–	–
CWM YSTWYTH MINE							
Effluent *a*							
11 June 1953	6·6	20	94	–	nd	10·6	132
27 October 1956	–	25	–	–	nd	–	–
3 November 1956	6·6	30	–	–	tr.	–	400
Effluent *b*							
11 June 1953	–	–	–	–	–	–	(dry)
27 October 1956	–	8	–	–	nd	–	–
3 November 1956	6·6	12	–	–	nd	–	240
Effluent *d*							
3 November 1956	6·8	18	–	–	nd	–	–
FRONGOCH STREAM							
20 May 1953	6·2	50	68	tr.	nd	–	830
31 May 1953	6·4	60	70	tr.	1 (?)	9·2	–
14 June 1953	–	50	82	–	tr.	–	420
20 June 1953	–	–	–	–	–	–	325
28 May 1956	5·8	65	90	tr.	tr.	–	–
13 June 1956	–	70	–	–	–	–	180
16 June 1956	5·8	90	120	–	nd	–	157
6 October 1956	–	40	–	–	–	–	–
STREAM DRAINING FROM WEMYSS MINE							
4 November 1956 p	6·6	6	–	–	nd	–	–
4 November 1956 q	6·6	3	–	–	nd	–	–
4 November 1956 r	6·8	2	–	–	nd	–	–

stream, at normal level, of 28·8 cu. ft/sec or a little less than 2 500 000 cu. ft/day. In full flood the water may rise 3 ft with a maximum surface velocity of about 6 ft/sec. A very rough estimate of the discharge under these conditions would be 44 000 000 cu. ft/day.

Some analytical data for the main stream at Llanfarian are included in Table 2. Further records for the zinc content at this station and the way it varies with the river level are shown in Fig. 3. Normal level is taken as the arbitrary zero selected in April 1953 as described later. Observations could not be made each day but the river was examined whenever changes in the weather made level changes likely.

It will be seen that the zinc concentration tends to fall when the level rises, recovering when the stream returns to normal. The relationship is not completely regular; it would appear that while rainy weather assists the washing out of soluble zinc in the dumps and the overflow of water in old shafts, the increase in the amount of zinc delivered by the effluents is more than counterbalanced by the increase in the volume of the main stream. Dry weather continued for long periods can concentrate the effluents but they may dry up completely. Thus *b* at Cwm Ystwyth, normally a swift stream 12-18 in. wide, had no flow in June 1953.

The most heavily polluted part of the main stream is its middle section, and samples taken at Grogwynion (Fig. 1) may have a zinc concentration of 1 mg/l. with the river at normal level. About 4 miles lower down the valley the stream which has its source at the Wemyss mine enters the Ystwyth; this tributary is still quite heavily polluted but its volume is not great and its zinc contribution is more

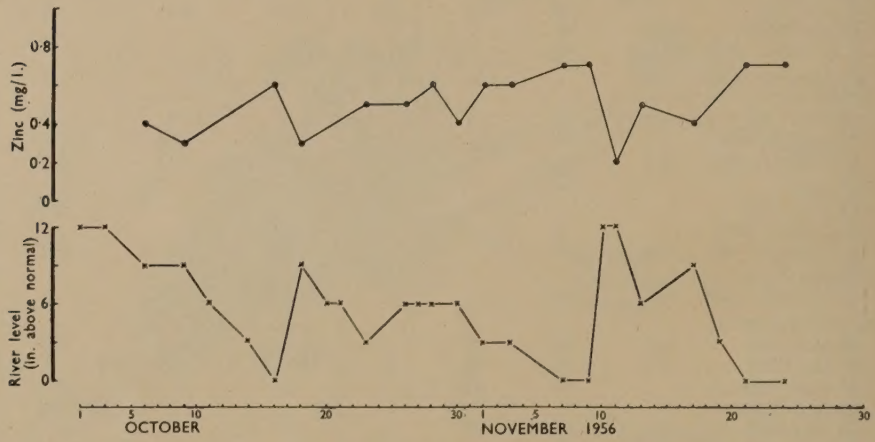

Fig. 3. Water level and zinc concentrations for the main stream of the river Ystwyth at Llanfarian, October and November 1956.

than balanced by further unpolluted tributaries before the river reaches Llanfarian.

In 1920 the Cwm Ystwyth and Frongoch mines employed about 88 men but in 1921 they were abandoned and since this time no mines have been worked in the Ystwyth valley. It has been noted that in 1921 the lower reaches of the river carried 0·4 mg/l. of lead in solution; the amount of zinc present may have been far greater than this. In 1940 the zinc content at normal level at Llanfarian was about 0·8 mg/l. and some of the effluents contained enough lead to pollute the main stream to a measurable extent. The present position, 35 years after the final cessation of mining activities and some 80 years after the peak period of the industry, seems to be that lead pollution is becoming negligible but that the zinc continues without great diminution. Speculation on the reasons for this is invited. Of the ores mined the silver ore was the most prized but the silver was rapidly exhausted; the lead was also valued highly and probably every effort was made, by

crushing and washing, to extract as much galena as possible before the discarded material was dumped. It is quite possible that great quantities of ore, not rich in lead or silver but containing a high proportion of zinc, were never washed but thrown on to the dumps or into old shafts. Furthermore, blende is a much lighter mineral than galena and so the simple water flotation process used in the early days of the industry, while effecting a reasonably good separation of lead ore from earthy matter, was far less satisfactory in the case of the zinc ore. Until oil flotation was introduced much more blende than galena must have run off to the

Table 3. *The fauna of the lower reaches of the main stream*

This list includes all the animals found in quantitative and qualitative samples taken at Llanfarian in April, May and June 1953.

PLATYHELMIA
Planaria vitta Dugés

HYDRACARINA
Mideopsis orbicularis (Müll.)
Atractides sp.
Sperchon sp.
Lebertia sp.
Hygrobates longipalpis (Herm.)

PLECOPTERA
Brachyptera risi (Morton)
Amphinemura cinerea (Oliv.)
Protonemura meyeri (Pict.)
Leuctra inermis Kemp.
L. hippopus Kemp.
L. fusciventris Steph.
Chloroperla tripunctata (Scop.)
C. torrentium (Pict.)
Isoperla grammatica (Poda)

EPHEMEROPTERA
Ephemerella ignita (Poda)
Baëtis rhodani (Pict.)
B. pumilis (Burm.)
Rhithrogena semicolorata (Curt.)
Heptagenia lateralis (Curt.)
Caenis sp.

HEMIPTERA
Velia currens (Fab.)
Gerris najas (Degeer)
Notonecta glauca L.

TRICHOPTERA
Sericostoma personatum (Spence)
Goera pilosa (Fab.)
Lepidostoma hirtum (Fab.)
Stenophylax stellatus (Curt.)
Hydropsyche instabilis (Curt.)
Plectrocnemia conspersa (Curt.)
Polycentropus flavomaculatus (Pict.)
Rhyacophila dorsalis (Curt.)
Glossosoma boltoni (Curt.)

COLEOPTERA (imagines)
Esolus parallelopipedus (Muell.)
Latelmis volckmari (Panz.)
Hydraena gracilis Germ.

COLEOPTERA (larvae)
Orectochilus villosus (Muell.)
Esolus parallelopipedus (Muell.)
Dryops sp.
Helodidae sp.

DIPTERA
Simulium reptans (L.)
Dicranota sp.
Chironomidae spp.
Atherix sp.
Tabanidae sp.

settling pits with the washing water. Lastly, blende is a much more stable compound than galena, undergoing oxidation and leaching out much more slowly; thus it is not surprising that a great reserve of zinc remains at the derelict mines.

THE FAUNA

Table 3 is a list of all the animals taken in quantitative and qualitative collections made in the Llanfarian area of the main stream. The insects are named as in the check-list of Kloet & Hincks (1945). Species in the list which were not found

in the quantitative samples are either very rare or have some habitat other than the stony bed (*Gerris*, *Velia* and *Notonecta*). Of the two species of *Chloroperla*, *C. torrentium* is rather less common than *C. tripunctata* and of the two species of *Baëtis*, *B. rhodani* is much more numerous than *B. pumilis*. All collecting was car-

Table 4. *Quantitative fauna collections for the stony main stream of the river Ystwyth, spring 1953*

The figures are numbers of animals per 2500 sq. cm.

	25 April	28 April	3 May	5 May	6 May	12 May	16 May	21 May	30 May	2 June	8 June	18 June
PLATYHELMIA												
Planaria	.	1	.	.	.	.	.	.	.	.	.	.
HYDRACARINA												
Mideopsis	.	.	.	2	1	.	.	1	1	.	1	1
Atractides	.	1	.	.	.	.	.	.	.	.	.	.
Lebertia	.	1	.	1	.	.	.	2	.	.	.	.
Sperchon	1	.	.	.	.	.	.	.	.	.	.	.
PLECOPTERA												
Isoperla	.	.	1	1	3	.	.	.	1	.	.	.
Chloroperla	68	42	20	30	22	16	18	18	11	18	3	12
Leuctra	1	3	2	4	.	.	.	.	.	7	14	11
Amphinemura	7	4	.	.	.	.	1	.	.	.	.	.
EPHEMEROPTERA												
Rhithrogena / *Heptagenia*	188	260	148	135	167	168	150	124	133	144	107	78
Baëtis	38	31	9	10	8	10	9	6	12	8	5	3
Ephemerella	.	.	.	.	.	.	.	.	2	2	2	8
Caenis	.	.	.	.	.	.	.	.	1	.	.	.
TRICHOPTERA												
Polycentropus / *Plectrocnemia*	.	2	3	2	5	3	.	4	8	.	3	4
Sericostoma	.	.	.	.	.	.	.	.	.	2	.	.
Lepidostoma	1	.	.	.	.	1	.	1	.	3	.	1
COLEOPTERA (imagines)												
Hydraena	.	.	.	.	.	.	1	1	.	.	.	.
Latelmis	1	.	1	.	1	2	4	4	2	1	7	3
Esolus	14	4	6	7	10	12	20	14	12	10	28	24
COLEOPTERA (larvae)												
Orectochilus	.	.	.	.	.	1	.	1	.	.	.	.
Esolus	22	17	6	5	4	3	4	5	.	3	5	3
Parnus	10	4	1	1	.	2	1	.	.	8	3	8
Helodidae	1	.	1	.	3	2	2	5	1	5	2	1
DIPTERA												
Simulium	.	1	17	6	4	.	3	2	2	.	3	3
Chironomidae	.	.	3	4	2	1	1	1	2	.	6	1
Atherix	.	2	.	.	.	1	.	.	.	.	.	.
Tabanidae	.	.	.	.	.	.	.	1	.	.	.	.
Total	352	373	218	208	230	222	214	190	188	211	189	161

ried out in the flowing water of the main stream; pools and small backwaters were not included.

A series of quantitative samples was taken in the spring of 1953. The results are set out in Table 4. The stony bed at Llanfarian is reasonably flat and uniform and well suited for quantitative work. The samples were taken exactly as described in the writer's study of the river Towy (Jones 1951, p. 75); a Surber type sampler was

used; this had an area of 500 sq. cm and on each occasion five collections were made from suitable parts of the stream-bed where the water was, very roughly 4, 6, 8, 10 and 12 in. deep. Even with the river at low level samples could not be taken where the current was swiftest, and at some points sampling was avoided because the current was not sufficient to wash the animals into the net. Nevertheless most of the river has, at normal or low level, a depth and current velocity suitable for this method. The material was examined as soon as possible and all animals seen with the naked eye were picked out and counted. The samples were free from mud and the use of sieves proved unnecessary. In counting the animals *Rhithrogena* and *Heptagenia* nymphs were not separated as many were very small or damaged and could not be identified with certainty. The results do not give a true indication of the numbers of *Simulium* larvae as these tend to be concentrated on large stones where the current is very swift. The Chironomidae were very few

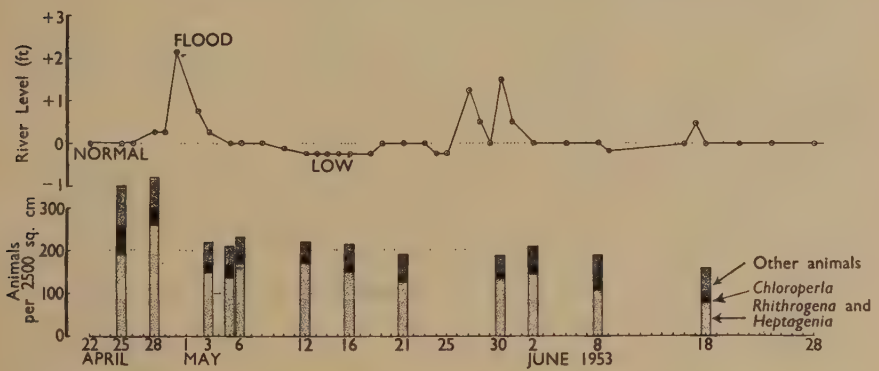

Fig. 4. Water level records for the main stream at Llanfarian, 22 April to 28 June 1953 and the results of quantitative sampling of the fauna of the stony stream-bed at the same station.

and small and no attempt was made to refer these to genera; most of them were Orthocladiinae and Tanypodinae.

In Fig. 4 the quantitative sample totals are set out against data for the river level compiled for the period of collecting. The weather was dry for about a week before 25 April and the level of the main stream on that date was taken as normal. Based on this arbitrary zero a scale was painted on the bridge at Llanfarian and used to read the river level on subsequent dates. As in the case of the 1956 records, the river was examined whenever weather conditions made level changes likely. The first two samples had totals of 352 and 373 animals/2500 sq. cm. On 30 April a sudden flood occurred and the subsequent samples showed smaller totals. The *Baëtis* nymphs seemed to be the chief victims; these insects are very nimble and can avoid being crushed by moving stones but have little capability for holding on against a swift current. The quantitative data for the Towy (Jones 1951, p. 78) show that flooding resulted in a drastic reduction in the numbers of *Baëtis* in July 1950.

Following the spate of 30 April the river remained at normal or low level until the end of May when two mild floods occurred. The sample of 30 May was taken in the morning, the 1½ ft rise came in the evening after heavy afternoon rain. Towards the end of the sampling period it was evident that the numbers of some of the insects were being reduced as a result of emergence; in the last sample nearly all the *Rhithrogena* nymphs were about to moult to the adult stage and juvenile *Chloroperla* and *Leuctra* nymphs had appeared.

Quantitatively the fauna does not compare badly with unpolluted, stony streams. The writer's samples from the Towy ranged from 40 to 1091 animals per

Table 5. *Summary of observations on the gut-contents of* Protonemura, Chloroperla, Isoperla, Rhithrogena *and* Simulium

The specimens were collected in April, May and June 1953 from the Llanfarian area of the main stream. The figures give the actual numbers in which the anterior part of the gut contained significant amounts of the 'foods' listed in the first column.

	Protonemura meyeri	*Chloroperla tripunctata*	*Isoperla grammatica*	*Rhithrogena semicolorata*	*Simulium reptans*
Number examined	5	50	25	45	35
Anterior part of the gut empty	–	–	4	–	–
Anterior part of the gut with contents digested	1	4	2	5	–
GUT CONTENTS					
Detritus and grit	–	6	–	40	35
Leaf fragments	4	5	–	1	30
Algae					
Green algae	–	2	–	1	12
Lemanea	–	–	–	–	1
Batrachospermum	–	2	–	–	15
Phormidium, *Oscillatoria*	–	5	–	–	–
Diatoms	–	1	–	8	28
Animals					
Rhithrogena, *Heptagenia*	–	29	5	–	–
Baëtis	–	4	1	–	–
Leuctra	–	4	–	–	–
Chironomid larvae	–	5	1	–	–
Simulium	–	4	15	–	–
Unidentified insects	–	3	2	–	–
Animal food only	–	38	19	–	–
Animal and vegetable food	–	3	–	–	–
Vegetable food only	4	5	–	40	35

2500 sq. cm. (Jones 1951). Butcher, Longwell & Pentelow (1937, p. 125) record average populations of 544, 847, 136 and 106 per sq. m for four stations on the Tees. Badcock (1949) in a study of tributaries of the Welsh Dee made thirty-one collections; some of these contained very large numbers of Chironomidae but in twenty-three instances the total number of organisms was less than 250/2500 sq. cm. The same author (1953) working on the Bråån and the Skogsmöllebäcken, tributaries of the river Kävlinge in southern Sweden, records benthic populations which for the most part do not greatly exceed those of the Ystwyth; the average for eleven samples from the Skogsmöllebäcken is about 580 2500 sq. cm.

Qualitatively the fauna is remarkable for what it lacks rather than for what it contains. The Oligochaeta, Hirudinea, Mollusca and Crustacea are still absent and the fauna is dominated by lithophilous insects. Trichoptera are still decidedly rare and there is a notable absence of the small Dytiscidae usually present in gravelly streams (*Bidessus*, *Deronectes* and *Oredoytes*). In seeking an explanation for the qualitative deficiencies of the fauna three main factors would appear to deserve consideration: the unfavourable physical nature of the river, direct toxic action by the polluting metal, and the nature of the food supply available to the animals. Physically the Ystwyth closely resembles the Rheidol which lies a few miles to the north. This shares with the Ystwyth the unfavourable features of soft, somewhat acid water, frequent floods and unstable, silted-up stream-bed but nevertheless has

Table 6. *The gut-contents of the Coleoptera*

The specimens were collected in April, May and June 1953 from the Llanfarian area of the main stream. The figures give the actual numbers in which the contents of the anterior part of the gut was of the nature specified in the first column.

	Latelmis volckmari (imagines)	*Esolus parallelo-pipedus* (imagines)	*Esolus parallelo-pipedus* (larvae)	*Parnus* sp (larvae)
Number examined	40	40	26	13
Anterior part of the gut empty	22	26	10	5
Anterior part of the gut with contents digested	–	–	5	–
Gut Contents				
Grit only	6	1	1	–
Grit and diatoms	2	13	3	–
Grit and amorphous matter	8	–	1	1
Grit and leaf-fragments	1	–	1	1
Grit, amorphous matter and diatoms	1	–	2	–
Grit, diatoms and green algae	–	–	2	–
Leaf-fragments only	–	–	1	6

a qualitatively rich fauna (Jones 1949a). It is possible that the metallic pollution may be responsible for the absence of Oligochaeta, Hirudinea, Crustacea and Mollusca but there is no reason to believe that the insect fauna is selectively limited by direct toxic action. The available experimental evidence (Davies 1941) would appear to indicate that zinc salts have little or no toxic effect upon aquatic insects. It is with the third factor that this study is more particularly concerned. During the period of quantitative sampling the feeding habits of some of the chief insects were investigated by examination of gut-contents. The methods employed have been described in my papers dealing with the food of insects in the rivers Sawdde and Rheidol (1949b, p. 152; 1950, p. 162). The results are set out in Tables 5 and 6; in the case of the beetles and beetle larvae the gut-contents displayed very little variety and it is possible to summarize the results on a basis of gut-contents type; rather more variety was seen in the species covered by Table 5 and here the figures give the numbers of specimens in which the different 'foods' were found.

Rhithrogena and *Simulium* subsist on their usual diet, the former on particles of

organic matter and small organisms brushed up from the substratum, the latter on similar material brought along on the current. Only five *Protonemura* nymphs could be found; this insect is much more common in autumn and winter and it may be presumed that good supplies of dead leaves are available then to furnish its usual food supply.

The *Chloroperla* and *Isoperla* nymphs seem to show an inclination to a more than normally carnivorous diet. In the writer's investigation of the feeding habits of these insects in the Rheidol it was found that 14% of the *Isoperla* nymphs had fed on vegetable matter only and 13% on vegetable and animal food. The corresponding figures for *Chloroperla* in the Rheidol are 44% and 32% (Jones 1950, p. 164). Hynes (1941, p. 530) states that 43% of the *Isoperla* specimens he examined had animal and vegetable food in the gut; his figures for *Chloroperla torrentium* and *C. tripunctata* are 43% and 49%. In the specimens from the Ystwyth every *Isoperla* with a recognizable gut-contents had fed on animal food only and so had thirty-eight of the fifty *Chloroperla* nymphs. The number of *Isoperla* specimens examined is not adequate but the insect is decidedly rare in the Ystwyth and a considerable amount of collecting was necessary to provide twenty-five; only six turned up in the whole series of quantitative samples.

In the case of the Coleoptera it will be noted that a high proportion had nothing in the anterior part of the gut. This would seem to indicate a shortage of food material. In July 1949 thirty imagines and thirty larvae of *Esolus parallelopipedus* from the Towy were examined, when the river supported a rich flora, and all the larvae and twenty-six of the adults had food in the gut (Jones 1951). Diatoms seemed to be the chief food of the Ystwyth *Esolus* but in most cases the number present in the gut was small. *Gomphonema parvulum* was the chief species. Butcher (1947) found that *G. parvulum* was one of the more resistant algae present in the river Tame, then polluted by toxic metallic salts. The same species was found by Reese (1937) in the river Melindwr, a lead-polluted tributary of the Rheidol.

Generally speaking the results set out in Tables 5 and 6 confirm the impression that the available plant food supply in the polluted reaches of the Ystwyth is decidedly limited in variety if not in quantity. Detritus seems to be the most important source of food and much of this may have its origin outside the main stream, in tributaries or in terrestrial vegetation. Dead leaves are probably available in quantity during the autumn and winter and from time to time a scanty supply of diatoms may be found on the stones, together with a little *Batrachospermum* and, perhaps, a little *Stigeoclonium*. Over the greater part of the lower and middle reaches of the river the stream-bed is too unstable for the *Lemanea* to become established; the alga grows thickly on the tops of firmly fixed stones in the deeper water but here the swiftness of the current probably prevents the insects feeding upon it. The absence of phanerogams is an important factor. Though *Ranunculus, Callitriche, Myriophyllum* and *Elodea* do not serve as a direct source of food, large beds of these plants strain out diatoms, desmids and other microscopic algae from the flowing water and provide a shelter for these organisms which multiply to form a good source of food for insects. Grasses like *Glyceria*

provide a good substratum for the growth of films of diatoms on which Trichoptera may 'graze'.

The factors responsible for the poor flora of the polluted part of the main stream require further examination. It has been pointed out that the unstable nature of the river bed seems to determine the distribution of *Lemanea*, and it is probable that the same factor operates against the establishment of phanerogams; the swiftness of the current is another obstacle. Newton (1944), in a review of botanical investigations into the effect of lead and zinc pollution upon stream vegetation, concludes that zinc is more injurious to plant life than lead, and Reese (1937) has shown that the scouring effect of grit and silt from mine dumps can have a pronounced effect on the microflora of a stream, particularly in the case of insecurely attached organisms.

Up to this point this paper has dealt only with the benthic animal population. Only two vertebrates are included in the fauna. The sea-lamprey, *Petromyzon marinus*, is an occasional visitor and brown trout now occur in the lower reaches of the river in small numbers; stocking is under consideration. Smaller fishes such as the minnow, stickleback and bullhead are absent. The critical concentration of zinc for the stickleback (*Gasterosteus aculeatus*) is about 0·3 mg/l. (Jones 1937) but the limits of toleration of *Salmo trutta* are not known. Affleck (1952) has claimed that zinc compounds are extremely toxic to the ova and alevins of brown and rainbow trout. Brown trout are apparently less susceptible than rainbow trout in the 'fingerling' stage (Affleck 1952, p. 152) and some acclimatization is said to be possible.

If the average rate of discharge of the main stream at Llanfarian and the average zinc concentration are taken to be 2 500 000 cu. ft or 70 000 000 litres/day and 0·6 mg Zn/l. the river brings down from the mines 42 kg of zinc each day or about 15 tons each year. The indications are that the pollution will continue for some time, with slow improvement. While it continues the flora and fauna must be expected to remain somewhat limited in variety. If the zinc concentration has reached a level which is not toxic to trout there is no reason why the river should not support a reasonable number of fish. The quantitative samples have shown that the benthic population is of the order of 800 animals/sq. m; as the average width of the mainstream is about 12 m this amounts to about 9 600 000 animals for each kilometre of the river's length.

SUMMARY

1. The river Ystwyth in north Cardiganshire continues to be polluted by effluents from derelict lead and zinc mines 35 years after the end of mining operations. Lead pollution has become negligible but zinc is present in the main stream near Aberystwyth in concentrations of 0·2-0·7 mg/l. according to river level.

2. The flora above the mines is rich, but below the sources of pollution seems poor in quantity and variety. The fauna is almost entirely made up of lithophilous insects. Quantitative sampling of the stony stream-bed near Aberystwyth in the

spring of 1953 indicated animal populations of 161 to 373 per 2500 sq. cm. *Rhithrogena semicolorata, Heptagenia lateralis, Baëtis rhodani, Chloroperla tripunctata* and *Esolus parallelopipedus* are the chief species.

3. The available food supply is very limited in variety. Detritus appears to be the main food source. Only 17 of the 279 insects examined had green algae in the gut.

4. Brown trout now occur in the river. The indications are that the pollution will continue, with slow improvement. Though limited in variety the invertebrate fauna seems quantitatively adequate to feed a reasonable number of fish.

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OBSERVATIONS ON THE ECOLOGY OF SOME BRACKISH WATER ORGANISMS IN POOLS AT SCARLETT POINT, ISLE OF MAN

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(With 1 Figure in the Text)

Investigations on the euryhaline species *Idotea chelipes* (Pallas) [= *viridis* (Slabber)] (Naylor 1955) led to observations on other brackish water organisms in pools at Scarlett Point in the Isle of Man. These observations are worthy of discussion in relation to the recent literature on the ecology of *Gammarus duebeni* Lillj. (Segerstråle 1946, Forsman 1951, Hynes 1954) and furthermore, they illustrate the fact that the two British species of *Jaera* have fairly distinct habitats. There appears to be little published information on the ecological relationship between *J. nordmanni* (Rathke) and *J. albifrons* Leach.

A series of three pools was studied in the igneous rock which fringes the tip of Scarlett Point; the approximate dimensions of the pools and their positions relative to each other are shown in Fig. 1. The lowest pool is situated at the head of a deep gully on an exposed part of the shore, and it opens to the gully by a narrow crevice 5 ft above MHWS. The middle pool is only about 6 in. above the level of the lower pool, while the upper pool is a further 3 ft higher. The depths of all three pools vary considerably, but each is between 2 and 3 ft at its deepest part. When there is any swell the funnelling action of the gully causes sea water to be forced into the lowest pool whenever the tide is above the level of about HWN. The amount of sea water entering depends upon the swell, and during storms so much sea water may be forced into the gully that the two lower pools merge completely.

A small flow of fresh water from a spring farther inland trickles through the pools and out through the gully into the sea. After heavy rain its flow is considerable.

PHYSICAL FACTORS

Water samples were taken from the surface and bottom of stations at which animals were collected, and their temperatures, salinities and oxygen concentrations were determined (Table 1). Salinity samples were estimated by titration against standardized silver nitrate in a brackish water burette, using the apparatus

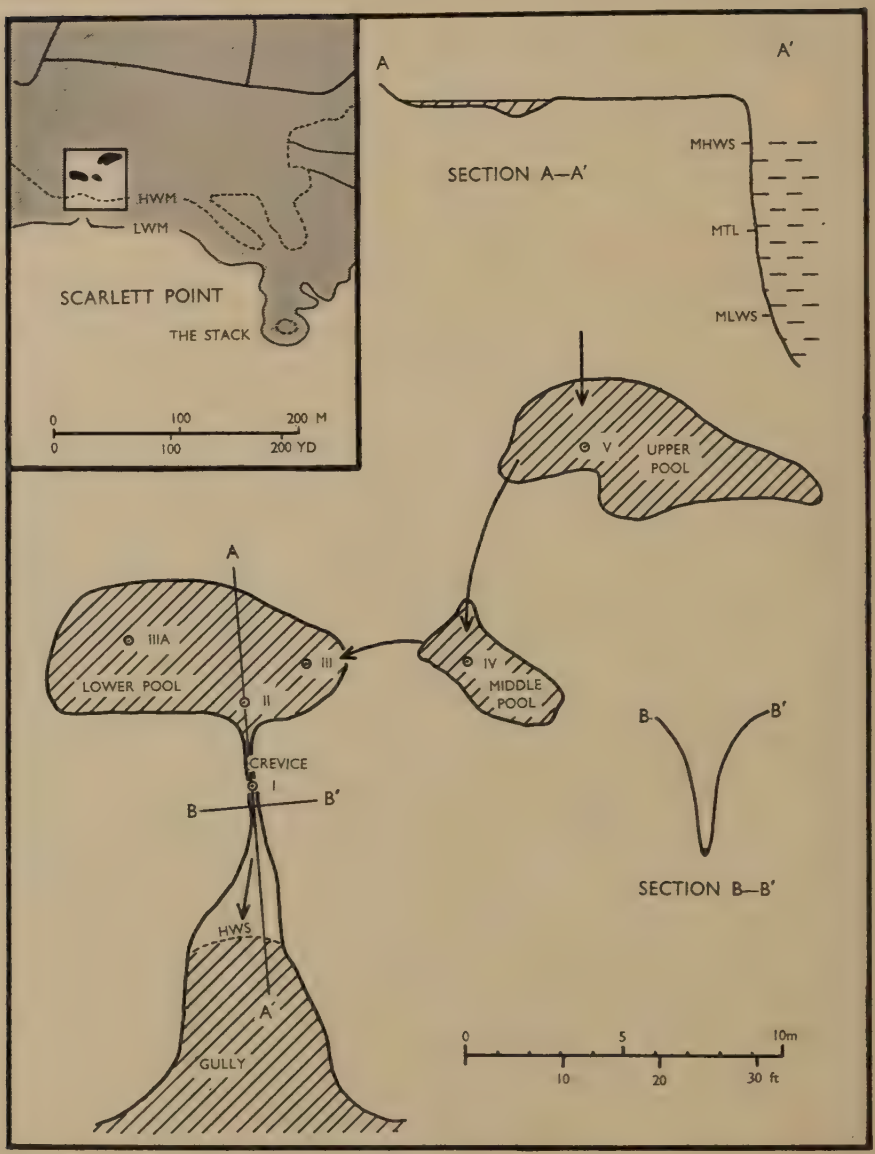

Fig. 1. Plan and sections of the pools at Scarlett Point. The horizontal and vertical scales are the same. Arrows indicate the flow of fresh water.

devised by Bather & Riley (1953) to detect the end point. Dissolved oxygen was estimated by the method of Winkler (Jacobsen, Robinson & Thompson 1950) and the percentage saturation calculated from the data of Fox (1907).

Table 1. *Temperature, salinity and oxygen concentration of the pools at Scarlett Point*

For station positions see Fig 1.

Station	Temperature (°C) surface	Temperature (°C) bottom	Salinity (‰) surface	Salinity (‰) bottom	Oxygen (ml/l.; % sat. in parentheses) surface	Oxygen (ml/l.; % sat. in parentheses) bottom
12 May 1953						
II	9·1	9·1	–	34·3	–	6.55 (100)
III	13·6	13·5	–	34·8	–	4.21 (71)
IV	13·1	12·7	–	19·2	–	5·16 (77)
V	12·4	12·5	–	12·2	–	6·39 (92)
18 January 1954						
II	8·6	8·6	33·3	33·4	7·65 (115)	7·65 (115)
III	–	–	–	–	–	–
IV	8·2	8·2	32·3	32·4	8·38 (123)	8·40 (124)
V	7·4	6·7	21·4	21·5	8·02 (107)	8·38 (112)
30 August 1954						
II	19·2	15·5	33·6	33·8	10·24 (187)	8·54 (148)
III	19·4	17·4	33·7	33·6	9·58 (175)	6·30 (111)
IV	17·6	16·1	33·8	31·7	7·81 (140)	7·58 (130)
V	18·2	16·9	2·2	2·2	8·64 (128)	8·73 (127)
2 November 1954						
II	8·3	11·3	1·6	29·2	8·30 (100)	2·35 (36)
III	8·4	11·1	1·5	29·4	8·28 (100)	2·69 (41)
IV	7·9	11·1	1·2	29·9	8·68 (104)	1·13 (17)
V	8·9	11·1	1·0	20·6	3·57 (44)	3·72 (53)
18 February 1955						
II	1·0	4·0	4·1	29·0	10·60 (108)	10·79 (141)
III	1·0	5·5	2·7	20·2	9·50 (96)	9·09 (117)
IV	2·0	5·0	1·9	22·1	11·42 (118)	10·94 (139)
V	0+	5·5	1·7	29·3	10·25 (101)	20·00 (275)
20 April 1955						
II	19·5	19·5	10·7	25·2	11·19 (181)	8·92 (157)
III	19·8	26·0	10·7	21·2	10·71 (173)	14·72 (280)
IV	17·0	23·0	5·3	11·0	11·24 (167)	14·81 (252)
V	17·0	23·0	5·0	13·3	8·41 (125)	18·30 (314)

(*a*) *Salinity*

Great quantities of sea water were observed sweeping up through the gully at high water on 19 January 1954, when force 6 winds were blowing on-shore. The two lower pools merged and water was also forced into the upper pool at this time. Such weather conditions had prevailed for some days, and samples which had been collected at low water on 18 January 1954 showed that salinity was high (21·4-33·4‰) and vertically uniform in all three pools. Thus no density layering was apparent, in spite of the fact that there had also been some rainfall; the effect of the

sea-water surges was sufficient to cause thorough mixing. On the other hand, rainfall in the absence of strong on-shore winds resulted in very marked density layering as the figures obtained on 2 November 1954 and 18 February 1955 show (surface 1·0-4·1 ‰; bottom 20·2-29·0 ‰). Lack of rain for some days before 20 April 1955, with moderate off-shore breezes resulted in higher surface salinities (5·0-10·7 ‰), but the bottom salinities on that day were quite low (11·0-25·2 ‰), presumably because there had been no recent marked influx of sea water. That some sea water had entered the lower pool at high tide is suggested by the high bottom salinity (25·2 ‰), and more particularly, the relatively low bottom oxygen concentration (8·92 ml/l.) at station II (see p. 17), but the influx was not sufficient to affect the remainder of the pool. The results for 30 August 1954 indicate that enough sea water had entered the lower pools to cause thorough mixing. The local meteorological records showed that the previous day had strong on-shore winds. Evidently the swell had been insufficient, however, to force sea water into the upper pool, where the uniformly low salinities suggested that there had not been any salt water invasion for some time.

Thus, in the pools away from the gully and even in the peripheral regions of the lowest pool, the salinity varied widely and irregularly. Occasionally, because of evaporation in the shallower parts of the lower pools, the salinity rose to values above that of sea water. On 12 May 1953 sea water, of salinity 34·3 ‰, entered the lowest pool near the crevice, but had little effect on the salinity at station IIIA some 15 ft away. There, where the water was shallower, the salinity rose from 36·0 ‰ to 38·6 ‰ in the six hours after high water, which occurred at 1100 h GMT.

(*b*) *Temperature*

The temperatures were also closely related to existing weather conditions, particularly in the shallower parts of the lower pools and the upper pool. Salinity layering was usually accompanied by thermal discontinuity as, for example, on 2 November 1954 (surface 7·9-9·9° C, bottom 11·1-11·3° C), whilst in the extreme case on 18 February 1955 all the pools were iced over. In summer, there were marked diurnal variations in temperature due to insolation. A rise from 15·5° C to 22·2° C over a period of six hours, for example, was recorded from the shallow station IIIA on 12 May 1953. A cool breeze, on the other hand, may reduce the temperature of the surface layers below that at the bottom since a discontinuity layer due to differences in salinity would prevent mixing.

(*c*) *Oxygen values*

Oxygen values were often very high, compared with the figure of about 5·7-7·7 ml/l. normally found for sea water in the area. These high values were presumably due to the photosynthesizing algae, and those for the bottom layers of all pools on 18 February 1955 (9·09-20·00 ml/l.) and 20 April 1955 (8·92-18·30 ml/l.) were probably exaggerated by the lack of circulation due to a marked discontinuity layer. Similarly on 2 November 1954, the low bottom values (1·13-3·72 ml/l.) may

have been due to decomposition of material thrown into the pool by rough seas about a week before the rain which formed the discontinuity layer. It may be significant that on this day some animals, such as *Procerodes ulvae* (Oersted), which usually prefer stones were found amongst strands of *Enteromorpha intestinalis* (L.) Link, where the oxygen tension would presumably have been higher.

Evidently the most variable conditions, particularly of salinity, occurred in the upper pool, and the most stable conditions (if they may be termed such) in the bottom layers of the lowest pool, particularly near the opening of the gully, where sea water entered at most spring tides. Salt water reached the other pools (and the outer regions of the lowest pool) only sporadically, and both temperature and salinity fluctuated very widely there. Fresh water from the stream tended to be confined to low salinity layers on the surfaces of the pools, and it was only in the upper pool that the salinity of the bottom water was frequently below 20‰. The continuous presence of relatively high salinity water (>20‰) at the bottom of the two lower pools must be of great importance to the fauna.

BIOLOGICAL FEATURES

The sampling methods were designed to give only roughly quantitative information about the fauna. If algae were present at the station enough were collected to fill a 1 lb jar (capacity 500 ml). If stones were present a 2 lb jar was filled with them. Each sample was sorted and the organisms counted in the laboratory (Table 2).

(*a*) *Algae*

The dominant algae in the pools were *Cladophora rupestris* (L.) Kütz., *Chaetomorpha aerea* (Dillw.) Kütz., *Enteromorpha intestinalis* and *Calothrix* sp. The first three species had characteristic zonal distributions in the two lower pools; *Cladophora rupestris* was restricted to the deeper, less variable parts, and to the crevice opening to the sea, *Chaetomorpha aerea* formed an intermediate zone around the two pools, and *Enteromorpha intestinalis* formed an upper zone which was subject to drying out and bleaching in hot dry weather. In times of heavy rainfall, particularly in spring, *Enteromorpha* extended into the connecting runnels between the pools, and some plants occasionally appeared in the highest of the three pools. For most of the year, however, the only alga in the uppermost pool was the small, tufted, *Calothrix* sp.

(*b*) *Animals*

Collections of animals were made irregularly during 1953-55. The dominant resident animals included the isopods *Idotea chelipes*, *Jaera nordmanni* and *J. albifrons*, the amphipod *Gammarus duebeni*, and the turbellarian *Procerodes ulvae*, as well as the stickleback *Gasterosteus aculeatus* L., oligochaetes, chironomid larvae and the copepod *Eurytemora velox* (Lillj.). Animals which were often washed into the pools, but which did not seem to establish themselves, included *Palaemon*

serratus (Pennant), *Carcinus maenas* (L.), *Hyale prevosti* (M-Edwards), *Gammarus locusta* (L.), and *Melita palmata* (Montagu). On the rocks at the seaward end of the lowermost pools were to be found *Patella vulgata* (L.), *Littorina saxatilis* (Olivi) and *L. neritoides* (Montagu), whilst living under stones in and around the pools were many specimens of *Ligia oceanica* (L.).

The distribution of the five dominant resident species is given in Table 2, in which numbers collected on each visit have been added together. The method of sampling did not permit an accurate assessment of seasonal variations in abundance, but these appeared to be generally slight. Only *Gasterosteus* showed marked seasonal fluctuation in numbers (see p. 22). All the dominant species bred in the pools, peak breeding for *Jaera*, *Gammarus duebeni*, *Procerodes* and *Gasterosteus* being mainly in spring and early summer. *Idotea chelipes* bred mostly in summer and autumn, as it did also in a saline lagoon in Essex (Howes 1939).

Table 2. *Total number of specimens found in a series of six samples in various months over the years 1953-55 at stations I-V (see Fig. 1)*

Station No.	*Jaera nordmanni*	*Jaera albifrons*	*Idotea chelipes*	*Gammarus duebeni*	*Procerodes ulvae*
I	4	692	72	61	22
II	86	180	430	121	8
III	264	34	88	108	25
IV	192	–	62	154	51
V	155	–	–	147	22

It will be seen that *Procerodes* and *Gammarus duebeni* were common in all the pools, and they were found to extend into the almost completely fresh water of the stream and system of small pools above station V. In a stream at a higher level than station V the distribution of *Procerodes* overlaps with that of *Planaria alpina* (Dana), whilst *Jaera nordmanni* and *Gammarus duebeni* were found farther upstream than *Procerodes* and occurred in pools with such typical fresh-water forms as *Nepa cinerea* L., *Gerris thoracicus* Schum, *Helobdella stagnalis* (L.), *Planaria alpina*, *Corixa venusta* (D. & S.) and *C. dorsalis* Leach. *Idotea chelipes* was restricted to the regions where algae were present, being particularly abundant in the deeper parts of the pools amongst *Chaetomorpha* and *Cladophora*. The two species of *Jaera* had characteristic though overlapping distributions; *J. albifrons* was more confined to regions which were regularly reached by the sea. While collecting the organisms, it was noticeable that whereas *Idotea chelipes*, *Jaera albifrons* and *J. nordmanni* preferred the shelter of weeds, *Gammarus duebeni* and *Procerodes ulvae* were most frequently found under stones, when both algae and stones were present.

The distributions of the resident species in the pools may now be compared with their usual distributions on the shore, in an attempt to determine the factors limiting their distribution.

(i) *Jaera nordmanni* and *J. albifrons*. Forsman (1949) and Bocquet (1953) described different habitats for various sub-species of *J. albifrons*, but there are

few published data on the comparative ecology of the two *Jaera* species. McCartan & Slinn (1953), however, have described the distribution of the two species in a stream running down the shore at Carnalea, Co. Down. In that locality, *J. albifrons* (= *J. marina* (Fabricius)—see Forsman 1949) extended from LWN almost to HWN whilst *J. nordmanni* extended from LWN to about 2 ft above HWS.

In the pools at Scarlett Point it is noticeable that *J. albifrons* was restricted to the seaward end of the lowest pool and to the crevice. *J. nordmanni*, on the other hand, extended through the upper pools and into the stream above station V, where it was found with typical fresh-water organisms (see p. 20). To compare this distribution with that of the two species on the open shore, some preliminary investigations have been carried out on populations of *Jaera* in the Isle of Man. These obervations, on various shores, have indicated that the upper limit of *J. albifrons* is about HWN whilst *J. nordmanni* extends to above HWS and is most abundant at HWN. This agrees closely with the observations of McCartan & Slinn at Carnalea.

In collecting *Jaera* on the shore, it was usual to find it in regions where there is a seepage of fresh water, and it is clear from this and the observations on the pools at Scarlett Point that both species are euryhaline, but that *J. nordmanni* is better able to withstand low salinities than is *J. albifrons*. In experiments in the laboratory *J. albifrons* died after less than 10 h in water of salinity of about 2‰ or less, whereas *J. nordmanni* was still alive after 70 h. Some *J. nordmanni* lived in tap water for up to 60 h.

(ii) *Gammarus duebeni*. This species is generally found in brackish water, particularly in pools above HWN (Segerstråle 1946, Forsman 1951). More recently Hynes (1954) has discussed the penetration of *G. duebeni* into fresh water in western Britain.

According to Forsman the type of brackish pool in which the amphipod predominates is one which is permanent, free from vegetation, reached by spray but not by surf, and receiving fresh water by seepage from higher levels. In the pools at Scarlett Point these conditions are best reproduced at station V and a little further inland. In these higher pools *G. duebeni* was one of the dominant larger organisms, while in the lowest pool, amongst the green algae, it was less abundant. The species was particularly common in regions where temperature and salinity were subject to the greatest variation, and it extended up the stream into the higher pools, where it was found with *Nepa* and other fresh-water forms (see p. 20).

(iii) *Idotea chelipes*. This is a euryhaline species, characteristically found in sheltered regions of brackish water at and above HWN and in estuaries (Naylor 1955). The lowest pool at Scarlett Point, though 5 ft above MHWS, receives surges of sea water almost as frequently as does a pool at HWN on a more sheltered and more gently sloping shore. As a result the pool provides the conditions under which *I. chelipes* usually lives, including water of changing salinity, a vegetation of green algae, and adequate shelter from the direct shock of waves (Naylor 1955).

(iv) *Procerodes ulvae*. In a fresh-water stream running over the shore at Wembury, Pantin (1931) found *Procerodes* (= *Gunda*) under fairly large stones from

LWN to HWN. Ritchie (1934) states that the upper limit of the species though generally at about HWN, sometimes extends above that level. McCartan & Slinn (1953) found that at Carnalea it occurred up to a level of about MHWS.

In the pools at Scarlett Point, *Procerodes* was present at all the stations sampled, and extended into the fresher water above station V, where it overlapped with *Planaria alpina*. Generally speaking the species was less abundant in the gully and the more uniform conditions of station II, than in the more variable conditions of the higher pools. It extended well above the upper limit of *Jaera albifrons*, but remained below that of *J. nordmanni*, as on the shore in the Isle of Man (see p. 21) and at Carnalea (McCartan & Slinn 1953). At Wembury Pantin (1931) found that there was a barren zone, roughly between HWN and HWS, which was completely devoid of animals. At Scarlett Point, however, and at Carnalea there was no such zone, for *Procerodes* overlapped with *Planaria alpina* and *Jaera nordmanni* extended into almost fresh water.

(v) *Gasterosteus aculeatus* (race 'B' of Heuts 1947). The stickleback was absent from the pools during winter, but by 21 April 1954 and 20 April 1955 large individuals had appeared in the two lower pools. On 21 April 1954 juveniles up to 1 in. long were also seen, but none were present on 20 April 1955. On 26 August 1955 large numbers of small *G. aculeatus* (1-1½ in.) were seen in the two lower pools, and a few in the upper pool. Thus it would seem that adult fish moved into the pools during spring to breed. In Belgium race 'B' occurs near the sea in waters of fairly high salinity; in autumn it migrates to the sea and reaches maturity, returning to the breeding grounds to spawn in the following spring (Heuts 1947). A similar migration behaviour may occur here.

DISCUSSION

The pools at Scarlett Point contain a wide variety of faunal types, including brackish rock pool animals, such as *Gammarus duebeni*, and several organisms characteristically found on the open shore. Because of the exposure of the shore and the funnelling effect which brings surf into the lower pool, conditions resembling those at HWN are created at a height of 5 ft above HWS, so that organisms such as *Idotea chelipes*, *Jaera albifrons* and *Procerodes ulvae* which are normally found below HWS on sheltered shores, are able to breed well above HWS. In addition, purely marine types such as *Palaemon serratus* are often found living in the pools, although they may not survive as breeding populations.

It has been shown (p. 19) that the most extreme variations of salinity and temperature occur in the highest pool. In the lower pools, the fresh water seems to flow in a surface stream, which passes over a reservoir of more saline water in the deeper parts of the pools. The upper layers and peripheral regions of the lower pools are therefore more variable than their deeper parts. The crevice and the deepest parts of the lowest pool are almost marine for much of the time, and the environmental changes there are never severe. Above the upper pool the conditions merge with those in a fairly typical fresh-water stream. These physical factors together with

that of light penetration appear to determine the zonation of the algae within the pools. *Cladophora rupestris*, typically an intertidal species, is confined to the crevice and the deeper parts of the lower pool. *Chaetomorpha aerea* and *Enteromorpha intestinalis* seem to be more tolerant of changing salinity and show more resistance to desiccation, for they form a middle and an upper zone respectively round the pools' margins.

The most abundant larger animal living amongst the algae is *Idotea chelipes*. Species of this genus are characteristically associated with algae. *I. chelipes* can tolerate a wider range of salinity than the other species of *Idotea*, and it is restricted to brackish water, apparently through competition with its less euryhaline relatives (Naylor 1955). When weed is absent this species is absent; it is more abundant on branched algae such as *Cladophora* than on *Enteromorpha*. It can be seen from Table 2 that the species is five times as abundant at station II, where the dominant alga is *Cladophora* than at station III where *Enteromorpha* is dominant. A similar preference for the shelter of branched algae has been demonstrated in the common shore idoteid *Idotea granulosa* (Naylor 1955). Thus it seems that a choice of suitable weed for food and shelter is an important factor governing the distribution of *I. chelipes*. It is not likely that the physical factors zoning the algae and causing *Cladophora* to be restricted to the deeper parts, are also restricting the *Idotea* directly. Unlike *Idotea*, *Cladophora* is as profuse at the head of gully (station I) as at station II, so it is clear that the physical factors limiting the distribution of each are not identical.

The distribution of the two species of *Jaera* seems to be less dependent upon the presence of algae. Although *Jaera* in the lower pools are more abundant amongst algae than under stones when a 'choice' of habitat is available (see p. 20), on the shore they are found more frequently under stones, as they are in the upper pool where algae are scarce. Forsman (1951) observed a similar difference in habitat of *Jaera*, which is found under stones on the open shore of the Swedish west coast, but which also lives amongst algae in rock pools and in the Baltic. Forsman suggests that the difference is due to the different competitive conditions in the two types of habitat, but here it may possibly be due to the *Jaera* seeking algae to avoid the more stagnant conditions under stones, as *Procerodes* appears to do when oxygen tension is low (see p. 19).

As for the relative distributions of the two *Jaera* species, the main concentration of *J. nordmanni* is in an environment too variable for *J. albifrons* to tolerate, and the former extends well away from the influence of the sea. This separation of habitats, with only a slight overlap, is to be expected from two such closely related species. Probably the more euryhaline *J. nordmanni* is excluded from the marine environment by direct competition with the less euryhaline *J. albifrons*.

As for *Gammarus duebeni*, experiments by Forsman (1951) support our observations regarding the wide tolerance of the species. Its lower limit would appear to be related to competition with other species (Beadle & Cragg 1940, Forsman 1951). It is generally less common in pools where algae are abundant (Forsman 1951, Segerstråle 1946). In the lowest pools at Scarlett Point the physical factors allow

algae to grow profusely and support an abundant fauna, and this seems to prevent *G. duebeni* from breeding prolifically. In the higher pools, however, which provide only fringe conditions for the most hardy of the larger green algae (*Enteromorpha*), *G. duebeni* establishes itself and grazes down the *Enteromorpha*. It is noticeable that when *G. duebeni* disappears from such pools owing to low temperatures or other reasons, *Enteromorpha* re-establishes itself. This has also been noted by Forsman (1951). The upper limit of *G. duebeni* has been studied by Hynes (1954) and seems to be related to direct competition with the fresh-water *G. pulex* (L.) when the latter is present. At Scarlett Point, where *G. pulex* was absent, *G. duebeni* was able to extend into fresh water. *G. duebeni* is therefore very euryhaline and its distribution seems to be limited largely by biological competiton.

Procerodes ulvae though mainly living under stones with *Gammarus duebeni* seems to be less tolerant of reduced salinity. On the shore its upper limit is well below that of the amphipod (McCartan & Slinn 1953). The turbellarian can survive without sea water for only about five days (Richie 1934), and at Scarlett Point it is confined to levels reached periodically by wave wash. Physical factors seem to be more important here, in restricting the distribution, than the possibility of biological competition with *Planaria alpina*.

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SUMMARY

1. Periodical measurements of temperature, salinity and oxygen concentration of both surface and bottom water, were carried out in a series of brackish pools at Scarlett Point, Isle of Man. The distributions of the larger members of the pools' flora and fauna were determined.

2. *Idotea chelipes* can tolerate wide salinity variations, but is limited by its preference for the shelter of branched algae.

3. *Jaera nordmanni* is more euryhaline than *J. albifrons* and is restricted to more variable habitats by competition with the latter.

4. *Gammarus duebeni* is most euryhaline, and is normally restricted to a very variable environment by competition with other species at each limit of its range, being able to extend into fresh water at Scarlett Point where *G. pulex* is absent.

5. *Procerodes ulvae* seems to be limited mainly by physical factors.

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MECHANICAL TIME-SORTING OF PITFALL CAPTURES

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(With 1 Figure in the Text)

During an investigation of the diurnal activity of the fauna of the floor in two contrasted habitats, preliminary estimates were made by counting, at regular intervals throughout the day, the number of animals seen to move in small quadrats. The limitations of this method soon became obvious. The weather was found to exert a controlling effect on the number of active invertebrates so that it was imperative, if valid comparisons were to be made, that the two habitats be sampled simultaneously. Further, critical scrutiny of small quadrats could only be maintained for about eight hours, even with rest pauses between observations, so that three periods of observation were needed to build up a single cycle of twenty-four hours. Allowing appropriate hours for sleep, this meant that four or five days were spent on each cycle, and during that period marked changes in the weather could occur and confuse the picture even within a single habitat.

A method was required which would allow simultaneous sampling of two areas and also give continuous sampling through a 24-hour period. The pitfall trap, long used by coleopterists, suggested itself as the best method of sampling the running fauna, with some mechanism for separating the catch into definite periods. The apparatus described below was designed to meet these requirements and may prove of use to other field workers in conditions where the sorting mechanisms described by Williams (1935) and Johnson (1950) are not suitable.

DESCRIPTION OF THE APPARATUS

The complete trap is illustrated in Fig. 1. The pitfall consists of a large can sunk into the ground with its mouth flush with the surface. Before the trap was made, containers of various shapes were tried out in the field and the behaviour of animals at the edge of the traps observed. It was found that the most complete catch was obtained when the mouth was sharply undercut so that there was no opportunity for an animal to recover its balance and thus escape. Consequently, the rim of the can is bent inward to achieve this result, though this introduces some difficulties when apparatus has to be passed through the narrow mouth. A 'Perspex' cover, supported around the periphery by six pins, is placed over the trap to prevent rain and debris falling in. Suspended from this cover is a metal disc, smaller in diameter than the mouth of the trap and level with its rim. This disc was included to prevent leaves and other material being blown in horizontally and blocking the mouth of the funnel below. Only rarely has litter been seen

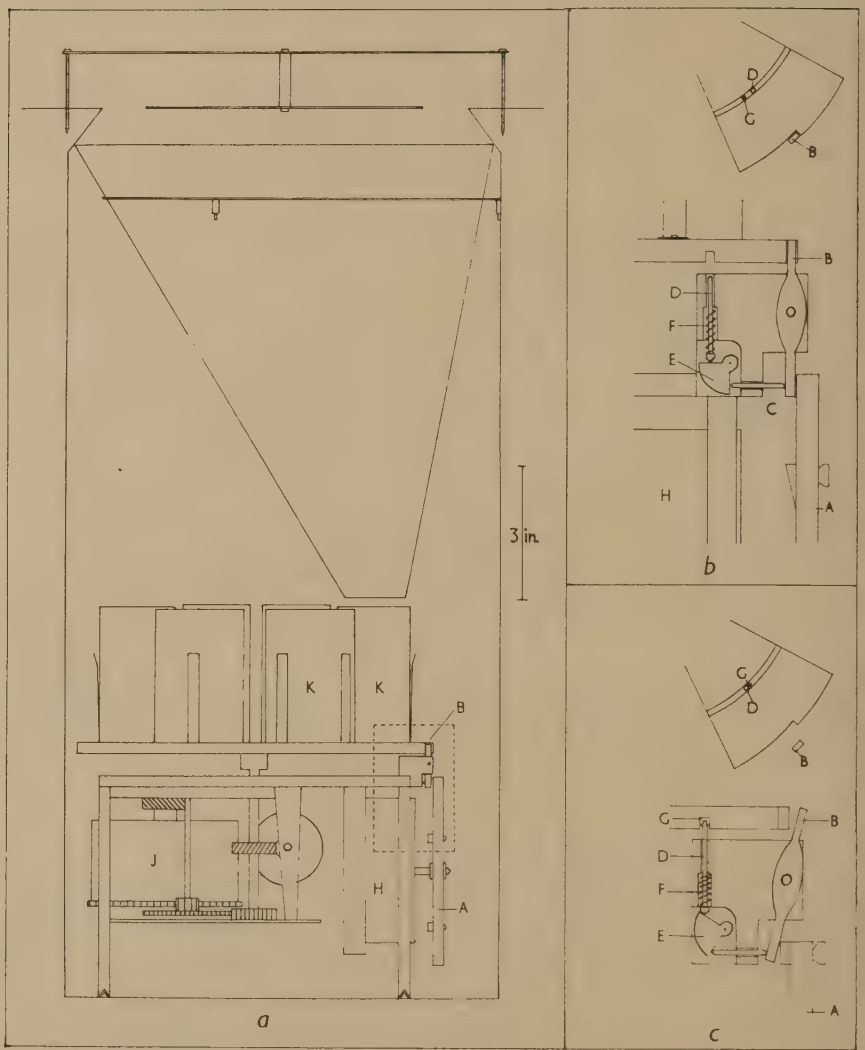

Fig. 1. (*a*) The time-sorting mechanism in position in a pitfall trap. For description, see text. (*b*) and (*c*) show the escapement in elevation and plan views of a sector of the turntable at each of the two stationary positions. A, timing disc; B, escapement lever; C, D, rods; E, intermediate cam; F, light spring; G, stop block; H, clock; K, K, pots containing glycerine.

on the disc, and it is doubtful if this precaution was necessary. One of the areas sampled was low-lying and liable to flood. As the water table rose during winter, the original can floated out of the ground. This difficulty was overcome by welding a flange to the base of the can and packing the earth tightly over the flange.

Within the can is an eccentric funnel, suspended by means of a wire ring which clips into three sockets on the wall of the can. The maximum slope of the funnel is 80° to the horizontal and the minimum slope, 60°. Acetate sheet was used to make the funnel which is sufficiently flexible to be distorted to pass through the narrow mouth of the can, springing back to its full size when in position. The smaller opening of the funnel is carefully registered over a pot containing dilute glycerine. The animals which fall into the trap are directed by the funnel into the pot where the fluid prevents both escape and predation.

Sorting of the catch into different periods is achieved by changing the pot at midnight, noon and an hour before and after sunrise and sunset. In this way, the day is divided into six periods. Movement of the pots is effected by a gramophone motor and the time of the change controlled by a Venner 24-hour clock. The gramophone motor and the clock are bolted to a small metal table so that the whole assembly can be handled as a unit. The gramophone turntable is replaced by a circular aluminium plate to which the six pots are fixed by spring lugs. The edge of the turntable is cut back opposite each pot to form a step which acts as a stop by engaging the escapement mechanism. To resist the impact of the escapement, the step is toughened by the insertion of a piece of gauge steel. The dial of the clock is replaced by an aluminium disc, which may be called the 'timing disc', to which are bolted six wedge-shaped shoes which act as cams to actuate the escapement. Near the edge of the timing disc is a slot along which the cams may be moved to allow for the varying times of sunrise and sunset.

The details of the escapement mechanism are shown in Fig. 1 which illustrates the escapement in elevation at its two extreme positions, together with diagrams of a sector of the turntable in plan view in each of the two stationary positions. The timing disc A, makes a complete anti-clockwise revolution in twenty-four hours, and as each cam reaches the top of its travel it rotates the escapement lever B. As the lever is depressed it is disengaged from the stop in the turntable, which is then free to move and thus change the pot beneath the funnel. If control of the movement of the turntable rests entirely with this escapement, a practical difficulty arises. To ensure that the escapement lever engages the next stop in the turntable, it must be completely free from the cam as soon as the turntable begins to move, and it must be heavily spring-loaded so that it will snap back into the resting position. But the clock will only function properly if the torque at the spindle is kept to a low value, and the loading required to re-engage the escapement immediately would stop the clock. These mutually exclusive demands are reconciled by the introduction of a secondary stop mechanism which comes into play as the escapement lever is progressively disengaged from the rim of the turntable. As the escapement lever, B is depressed by the cams, it moves rod, C, which, in turn, raises rod D, via the intermediate cam E. Rod D rises into an

annulus cut into the underside of the turntable, so that the table is free to rotate until rod D is met by a block G in the annulus situated beneath a pot. In this way the next pot is retained beneath the funnel although the escapement lever is still disengaged. When the lever is freed by the cam, the light spring F, forces down the rod of the secondary escapement and re-aligns the escapement lever to engage the edge of the turntable. During this movement, the pot travels about ¼ in., but as the opening of the funnel is smaller than the mouth of the pot, the funnel effectively directs the catch in either position. The turntable may thus be held stationary by either the escapement lever B, or the rod D, and both positions are figured.

The apparatus has proved to be very robust. As the interacting parts are bolted to a common stand, no adjustments have to made in the field. The work done by the clock should be kept to a minimum, and to this end the travel of the escapement lever should be kept small, and frictional losses reduced by bevelling the face of the escapement lever and by keeping all sliding parts bright and oiled. Cleanliness of the secondary escapement is extremely important as the spring is purposely kept light. Dirt and rust in the annulus can hold up the pin against the action of the spring, and it would be worth while making the blocks in the annulus of stainless steel. In the models which are in operation, this has not been done and most of the work of maintenance is the cleaning of these blocks.

THE EFFECT OF THE FUNNEL ON THE CATCH

The use of pitfall traps constitutes a selective method of sampling, as may readily be confirmed by watching the movements of the ground fauna in the vicinity of such a trap, and results obtained by this means have to be checked by some other sampling method. The trap described above introduces a further selective factor by the use of a funnel which may permit some animals to recover their balance and escape. Consequently, the effect of the funnel on the catch was determined in a field experiment during the summer of 1954. In previous work with pitfalls, the catch had been inactivated, not by glycerine but by a smear of 'Stictite', a commercial grease-banding material which proved effective for arresting the movement of all animals other than molluscs. Stictite has a strong smell, and the catch has to be picked out by visual inspection of the smear, both possible sources of error. The experiment included the comparison of Stictite and glycerine, in addition to the comparison of traps with a funnel and traps without a funnel. Although the former comparison is not pertinent here, it is included as the experimental lay-out was determined by the double comparison.

Eight cans were sunk into the ground, each covered by a lid held about an inch from the ground by three legs. The cans used by confectioners for fats and jams were found to be suitable, the margins being bent inwards to give an undercut mouth as in the trap described above. All the cans were sited in a copse of about ten acres, four cans among thick litter under a canopy of oak and hawthorn and four in a part of the copse where the canopy was not complete so that the litter layer was thin but a well-marked field layer was present. In each set of four cans,

Table 1. *The numbers of animals caught per week in an experiment to determine the effect on the catch of a funnel and the grease-banding material 'Stictite'*

P, trap without funnel; F, trap with funnel; G, trap with glycerine; S, trap with Stictite.

SQUARE ONE

Trap Number	1				2				3				4			
Week	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Treatment	PS	FG	FS	PG	PG	FS	FG	PS	FG	PS	PG	FS	FS	PG	PS	FG
Chilopoda	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Diplopoda	1	8	3	6	4	4	4	1	1	0	3	1	7	1	0	0
Isopoda	1	1	0	0	1	1	4	0	5	0	1	0	2	1	1	2
Opiliones	2	0	6	5	5	2	4	5	9	5	2	1	3	3	11	3
Oribatei	13	33	64	69	15	22	28	69	2	16	21	23	2	12	38	33
Other Acarina	2	13	7	4	5	13	0	5	1	0	4	3	3	14	8	5
Araneida	10	14	14	11	12	20	2	11	15	12	13	25	18	27	19	10
Collembola	13	25	7	19	17	5	8	22	19	14	8	6	2	17	7	23
Carabidae	17	6	3	2	7	3	3	1	10	2	2	1	13	7	3	9
Staphylinidae	13	27	7	3	22	18	4	7	15	17	9	2	31	43	13	5
Other Coleoptera	3	3	3	1	4	1	7	6	7	2	2	2	1	2	1	2
Larval Coleoptera	0	19	6	3	8	7	8	2	3	7	6	1	2	15	2	9
Diptera	11	3	2	5	4	11	1	17	8	7	5	7	10	9	15	4
Larval Diptera	3	1	0	1	2	0	0	0	0	0	1	0	1	0	0	0
Hemiptera	0	1	0	2	1	1	0	2	1	1	0	0	0	1	1	4
Parasitic Hymenoptera	5	5	2	10	3	3	2	4	12	12	10	8	6	22	4	6
Other Arthropoda	3	3	0	2	0	3	1	2	0	1	1	3	7	4	9	9

SQUARE TWO

Trap Number	1				2				3				4			
Week	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Treatment	FS	PG	FG	PS	FG	PS	FS	PG	PG	FS	PS	FG	PS	FG	PG	FS
Chilopoda	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0
Diplopoda	5	3	0	0	2	1	0	3	2	2	0	1	3	3	2	1
Isopoda	0	3	3	2	1	1	3	2	2	1	1	0	2	3	0	0
Opiliones	2	5	1	6	1	3	1	1	5	8	4	5	2	5	5	1
Oribatei	3	18	14	29	3	13	15	18	5	3	14	5	7	5	22	6
Other Acarina	1	3	3	8	0	2	2	4	1	4	0	1	2	4	5	5
Araneida	10	14	6	7	13	13	17	6	12	21	8	9	13	6	6	11
Collembola	8	4	10	3	26	11	5	17	18	4	6	7	18	20	36	15
Carabidae	10	6	4	1	10	3	4	3	3	8	4	3	14	4	2	1
Staphylinidae	11	11	0	6	13	7	6	1	22	15	7	7	20	28	14	3
Other Coleoptera	2	4	3	4	2	3	4	4	10	1	1	1	4	2	1	0
Larval Coleoptera	0	9	6	10	0	4	2	1	6	8	8	5	0	11	3	4
Diptera	24	14	7	8	5	9	8	4	14	9	8	7	25	5	4	12
Larval Diptera	10	0	0	0	3	0	0	0	2	0	1	0	2	0	0	0
Hemiptera	0	0	0	1	1	2	0	0	0	0	1	0	0	0	2	0
Parasitic Hymenoptera	3	15	7	4	6	3	1	9	10	2	0	4	1	2	2	1
Other Arthropoda	4	4	1	1	5	1	1	4	5	0	2	1	8	0	2	1

the four possible combinations of treatments were represented during each sampling period, one can receiving Stictite with a funnel, one Stictite without a funnel, one glycerine with a funnel, and the remaining can glycerine without a funnel. The traps were left in operation for a week at a time and the experiment continued for four weeks so that each individual can received each of the possible treatment combinations. In this way, the results could be analysed as two Latin squares. For the experiment, symmetrical funnels of acetate sheet were made with a slope of 60° to the horizontal, equal to the lesser slope of the funnel used in the time-sorting trap. The funnels were supported on tripods standing on the bottom of the can. The Stictite was smeared on to bakelite discs and the glycerine contained either in a jar for use with the funnel or in metal dishes which could be assembled inside to form a continuous ring of glycerine under the margin of the tin.

Table 2. *The results of analyses of variance on the more numerous groups in Table 1, after transformation of the counts to log.* (n+1)

n, not significant; S, significant at the 5% level; HS, significant at the 1% level.

Source of variation	d.f.	Diplopoda	Isopoda	Opiliones	Oribatei	Other Acarina	Araneida	Collembola	Carabidae	Staphylinidae	Other Coleoptera	Larval Coleoptera	Diptera	Parasitic Hymenoptera
a. Between squares	1	n	n	n	S	n	n	n	n	n	n	n	S	n
b. Between traps within squares	6	n	n	n	HS	n	n	S	n	S	n	n	n	HS
c. Between sampling periods	3	n	n	n	HS	n	n	n	HS	HS	n	HS	S	HS
d. Funnel v. no funnel	1	n	n	n	HS	n	n	n	n	n	n	n	n	S
e. Glycerine v. Stictite	1	n	n	n	n	n	n	HS	n	n	n	S	HS	HS
f. Interaction ($d \times e$)	1	S	n	n	n	S	S	n	n	n	n	n	n	n
g. Error	18													
h. Coefficient of variation		50	75	41	13	45	13	19	24	22	40	36	19	20

The catch was picked out of the Stictite or filtered from the glycerine, the final inspection in either case being made under the binocular microscope. Animals were classified into the groups listed in Table 1, groups which were compiled partly to meet the need for adequate numbers for statistical analysis and partly reflecting the special interest of the project of which this is a part. Table 1 gives the details of each catch and where the numbers of animals in a group were sufficiently large, an analysis of variance was performed, the counts first being transformed to log $(n+1)$ as the raw counts were non-normal. In Table 2, rows *a* to *g* illustrate the type of analysis and summarize the results for the various groups. The error variance was used to test the interaction of the main treatments and the variance between traps within squares. If either of these was significantly greater than the error variance the main treatment effects were tested against the interaction and the variance between squares against the variance between traps within squares. Otherwise, the error variance was used throughout for the calculation of F, the

variance ratio. Instances where the differences between the main treatments were significant are discussed below.

Oribatei. Plain traps caught 1·5 times as many oribatids as did the traps with funnels, so the type of trap described in this paper would significantly underestimate the number of oribatids falling in. The cause of this difference was almost certainly the accumulation of dirt or damp on the surface of the funnel while the trap was in operation. Despite thorough polishing beforehand the funnels were always dirty when brought in from the field and this film would serve to halt the free fall of the mites and permit them to escape. The present regime of sampling with the time-sorting mechanism requires a sampling period of only 24 hours and the funnels remain clean during that time.

Collembola. Traps with glycerine gave counts 1·5 times those using Stictite as the holding substance. Such a result would be expected after a little experience of picking the catch out of Stictite, for not all the springtails can be successfully isolated. These soft-bodied insects readily disintegrate leaving only a grey pool to mark the original capture. It is likely that the original catch was the same but that separation by filtration from glycerine was a more effective method than hand picking from a greasy film.

Larval Coleoptera. Although the differences between Stictite and glycerine are significant for this group, extended examination of the counts by the *t* test shows that the differences are only real when the comparison is made between traps with funnels. As the combination of funnel and Stictite is not used in any of the sampling series, this difference may be ignored.

Diptera. Stictite counts were twice the glycerine counts. In the laboratory and the field it is obvious that flies are attracted by the odour of the grease which explains this discrepancy.

Parasitic Hymenoptera. Both the main treatment effects were significant for this group. Glycerine counts were 2·5 times those with Stictite indicating that Stictite acts as a repellant or that the total catch was not picked out. The latter alternative seems the more probable when the two catches are compared qualitatively, for the main difference is in the abundance of such fragile forms as the Mimaridae which, like the Collembola, readily disintegrate in Stictite. For the comparison between traps with and without funnels it must be remembered that the alate Hymenoptera do not literally fall into the traps. They may be observed flying just above the litter, occasionally alighting and running over and under the fallen leaves, or flying into crevices. If they pass beneath the lid of the trap, the smooth sides of the funnel would provide no positive sensory cues to stimulate further investigation so, to this extent, the funnel acts as a deterrent, reducing the number caught to 0·6 of the true value.

For the remaining groups, when the interaction effects were significant the four combinations of treatments were examined by the *t* test, bearing in mind that two of the combinations are not used for routine sampling. The only pertinent differences were found in the Diplopoda, where four times as many millipedes were caught in plain traps with glycerine as in plain traps with Stictite. In this instance,

the difference cannot be attributed to the difficulty of picking out the millipedes from the grease as the head capsule is easily visible under the binocular microscope. It is concluded that Stictite does repel millipedes and observation of millipedes near pitfalls showed that their slow progression over the edge of the trap would allow ample time for olfactory stimuli to act.

To summarize, the use of a funnel in a pitfall will reduce the number of oribatid mites and parasitic Hymenoptera only. If the ratios found in the present investigation be accepted as giving the order of the magnitude of the error, then they may be used to give correction factors of 1·5 and 1·6 respectively.

RELIABILITY OF PITFALL ESTIMATES

Sampling moving animals by means of a limited number of fixed traps is an erratic process which gives highly variable results. In Table 2, row *h* gives the coefficients of variation (100 × standard deviation/mean) for the different groups

Table 3. *The numbers of woodlice caught in simple pitfall traps*

Each figure represents the sum of three consecutive catches, and the analysis of variance has been performed after transformation to log. $(n+1)$. Levels of significance are indicated as in Table 2.

Area	Trap	February-April	April-July	July-September	October-December
Wood	*a*	1	8	18	4
	b	2	3	1	2
	c	1	1	0	2
Scrub	*a*	0	24	2	1
	b	0	4	5	0
	c	1	13	5	0
Ley	*a*	0	1	0	0
	b	0	0	0	0
	c	0	6	5	2

Source of Variation	d.f.	Variance	Significance
Periods	3	0·5161	HS
Areas	2	0·3657	n
Habitats within areas	6	0·2220	S
Interaction *a* × *h*	6	0·1455	n
Interaction *a* × *c*	18	0·0663	

tested statistically, and lack of significance is found where the coefficients are high. It may be objected, therefore, that the paucity of significant results in the above experiment is the result of such variation and it remains to be demonstrated that the pitfall method is sufficiently sensitive to reveal real differences. Such differences would be expected between samples taken at different seasons and between samples from different habitats; if these differences were not detected by pitfalls then the method would be worthless.

As a background to the investigation of diurnal activity, and to compensate for the lack of replication with the time-sorting type of trap, pitfalls had been in

operation for a year in three main areas, a wood, a newly seeded ley and open scrub. In each of these three areas, three pitfalls traps were laid, distributed to sample the main habitats presented; *e.g.* the wood consisted of oak and hawthorn to the south of a ride and alder to the north, so one trap was placed under each of the three main tree types. In the scrub, one trap was placed near the boundary hedge and the other two at different distances from clumps of bushes. The traps were in operation, simultaneously, for a week at a time, the catch being inactivated by Stictite smeared on to bakelite rings, and one week in four was sampled throughout the year.

The woodlice may be considered as a test case. They show the highest coefficient of variation in Table 2 and they are a convenient group in that a single species, *Philoscia muscorum* (Scopoli) makes up the catch. The numbers caught were low, so to make them more susceptible to statistical treatment, three successive samples were summed for each trap. The numbers so obtained are displayed in Table 3, together with the analysis of variance of the data after transformation to log. $(n+1)$. The coefficient of variation is still high, ($= 64$) but despite the large variation, significant differences are obtained. The difference between catches at different times of the year is highly significant, *i.e.* at the level $P = 0{\cdot}01$, while differences between catches from the different habitats within the larger areas are significant at the level $P = 0{\cdot}05$.

It may be concluded that sampling by pitfall traps, despite the inherent variability, is sufficiently sensitive to show up real differences of ecological significance.

ACKNOWLEDGMENTS

I am indebted to Mr B. K. Bull, one-time head of the instrument workshop, Reading University, for translating into a practical machine my theoretical requirements.

SUMMARY

1. A mechanism is described which is incorporated into a pitfall trap to separate the catch into six periods of activity during the day.

2. An experiment to determine the bias of the trap showed that underestimates are made of the number of oribatid mites and parasitic Hymenoptera. Of the seventeen groups into which the catch was classified, these were the only two giving wrong estimates.

3. Pitfall traps are shown to be sufficiently reliable, in the statistical sense, to reveal the differences in the number of animals caught at different times of the year, and in different habitats.

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MOVEMENTS OF INDIVIDUAL MEMBERS IN A POPULATION OF THE SHORE CRAB, *CARCINUS MAENAS* L., IN THE LITTORAL ZONE

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(With 4 Figures in the Text)

As shown by Williamson (1900) and Meek (1913) the edible crab, *Cancer pagurus* Linn., undertakes an annual long-range migration into deep water during the winter months and returns to shallow water during the summer. A similar migration is also undertaken by the shore crab, *Carcinus maenas* L., which is not found in the littoral zone during the winter months, and on the south coast of Britain makes its first appearance in early April. From April onwards throughout the summer, specimens can be found at all levels from high-water mark down into the sublittoral zone and it is generally assumed (*e.g.* Yonge 1949, p. 207) that they 'range at will over the shore'.

It is obvious that, being active animals they are physically capable of such a feat during the period of high tide, but unless they are disturbed they do not wander over the shore at low tide. As the tide recedes they either go back with it into deeper water, or seek shelter under rocks and seaweed. Those which seek shelter will be subjected to severe adverse environmental conditions, and the higher up the shore they are, the longer and more severe these conditions will be. It is not unreasonable to suppose that some individuals are better able than others to withstand these conditions. If this were so, a kind of zonation might exist at low tide in which the upper levels of the shore are inhabited by crabs whose physiological constitution differs in some way from that of crabs which are confined to the lower levels. Physiological differences have in fact been demonstrated in molluscs taken from different levels by Segal, Rao & James (1953). Heart-beat, condition of gonads and shell-weight relative to weight of soft parts were found to vary systematically with intertidal level, in two species of limpet, *Acmaea scabra* and *A. limatula* and in one species of mussel, *Mytilus californianus*, even when the distances involved were no more than a few feet. Evidence that similar differences may exist in shore crabs was provided by Drzewina (1908 *a*, *b*) who described behavioural differences existing between crabs collected at high levels and those collected lower down the shore. She found that when taken from their hiding places and released in the open, crabs from upper levels displayed a strong, positive hydrotactic response and hence walked towards the sea, whilst those taken from lower levels showed no hydrotaxis but were negatively phototactic and sought shelter under rocks and seaweed.

The aim of the experiment described in this paper was firstly to discover, by

tracing the movements of marked individuals whether the crabs wandered at random over the shore or showed any tendency to remain in one particular zone; and secondly, by measuring specimens, to find if any morphological differences could be detected between crabs taken at different levels.

LOCALITY

A suitable locality was found at Chilling on the eastern shores of Southampton Water where there is a wide flat expanse of mud and sand on which stand three artificial rocky areas. Two of these areas, designated A and B, are the remains of a boom defence erected during the 1914-18 war and the other, C, is the broken remains of the drainage outfall from a small fresh-water lake. All three areas have, therefore, been in existence for a very long time. Areas A and C are situated just below the level of mean high-water neap tides and the other area, B, is situated just above mean low-water neap tides. Areas A and C are 110 yd apart, whilst area B lies between them and 120 yd off-shore. Area A is 375 sq. yd in extent, being in the shape of a rough diamond whose axes measure 30 yd by 25 yd with the long axis at right angles to the beach. It is composed of rocks and slabs of concrete covered with *Fucus spiralis*, *F. vesiculosus* and some *Ascophyllum nodosum*. At neap tides the sea begins to cover the rocks 2 h 20 min before high water, and leaves them again 3 h 15 min after high water, so that the area is submerged for rather less than 6 hours in every 12. Area C is much smaller and is roughly triangular in shape having an area of 110 sq. yd. It is composed of a few rocks and many concrete slabs which are sparsely covered with equal amounts of *Fucus spiralis* and *F. vesiculosus*. Being slightly lower down the shore than area A it is covered by the tide for rather more than 6 hours in every 12. Area B is different from the others, not only because it is situated off-shore but because it is composed of lumps of chalk, slabs of iron, the remains of wooden piles and only a few rocks. It has a total area of 875 sq. yd and the timber is thickly covered with *F. vesiculosus* and *F. serratus*. The tide covers the area 4 h 30 min before high water and uncovers it again 4 h 30 min after high water so that it is submerged for 9 hours in every 12.

At low tide, crabs are found sheltering under the rocks etc., and hiding under the seaweed in all three areas. Unless disturbed they remain there until the tide comes in again and covers the area, when they can be seen emerging and foraging for food. When the tide recedes they return again to shelter. For many hundreds of yards in each direction there is no other place in which crabs could find shelter unless they buried themselves in the mud. But they only do this if they are disturbed from their normal hiding places under rocks. Crabs which do not reach the shelter of rocks before the tide recedes must therefore go out with it into the sublittoral zone, though they may return again at the next high tide.

TECHNIQUE

The method of marking release and recapture developed by Fisher & Ford (1947) in their studies of butterfly populations seemed to be particularly suitable for this

type of work as it gives not only an estimate of the size of a population but also an indication of the 'survival rate'.

In preliminary experiments, marks were made on the carapace of the crabs with cellulose paint in the manner described by Fisher & Ford (1947) and one which has proved successful for a number of terrestrial animals. But with crabs this is only successful if the carapace can be dried completely before the paint is applied and on an open beach in wet weather this is not possible. The crabs were therefore marked by removing with a pair of scissors a small part of one of the teeth on the anterior and antero-lateral margins of the carapace. This appears not to affect the crab adversely even when a number have been removed. Teeth are often damaged in this way in nature, but whereas the natural damage always has a jagged edge,

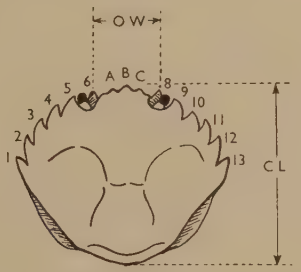


Fig. 1. Carapace of shore crab, showing the teeth used for indicating date and area of release. The measurement CL (carapace length) and OW (optic width – the distance between the suboptic teeth) were made on crabs captured in April, May, July and August.

the cut made with scissors is always smooth and straight and no difficulty was ever found in deciding whether a particular mark had been made with scissors or otherwise. The advantage of this method over the use of coloured paint is that it is permanent until the crab moults, and since the marks can only be seen when the crab is inspected closely, there is no tendency to select marked crabs in preference to unmarked ones when a number of them are found together under the same rock. The marking code used for the experiments is shown in Fig 1.

The technique adopted when collecting was to work across the chosen area in a fairly systematic way turning over suitably sized rocks, taking care to ensure that every crab found underneath was captured. The crabs were put into a sack and the rocks replaced as nearly as possible in their original position. At the end of half an hour collecting in this way, the crabs were removed one by one and any having a carapace length of less than 30 mm were discarded. This was done partly because small crabs moult more frequently than large ones and partly because they are likely to be more static than larger ones. Crabs of 30 mm and more were marked in accordance with the predetermined code (Fig. 1), each crab being given two marks, one to indicate the date and the other to indicate the area from which it

was captured. A record was kept of all the marks placed on crabs and of those found on recaptured specimens.

After marking, the crabs were released in the centre of the area from which they were taken and soon scurried to shelter under rocks. Any crabs which were sluggish in their movements or which were damaged in any way were killed and their bodies removed from the shore. Out of a total of over 1600 crabs captured it was necessary to dispose of only 43 in this way.

During the period 1 to 6 and 8 to 13 August, inclusive, crabs were captured, marked and released in each area once every day. This meant that the rocks were covered by the tide at least twice between collections, and the crabs had plenty of time in which to move about. There was no evidence of a tendency to congregate near the release point. During the period 15 to 18 August inclusive collections were made in each area in the same way as previously, but the specimens were removed from the shore and measured, a record being kept of any marks they bore.

RESULTS

(*a*) *Recaptures*

The total number of crabs marked and released during the experiment was 1195 (821 males and 374 females), the number captured was 1653 (1118 males and 535

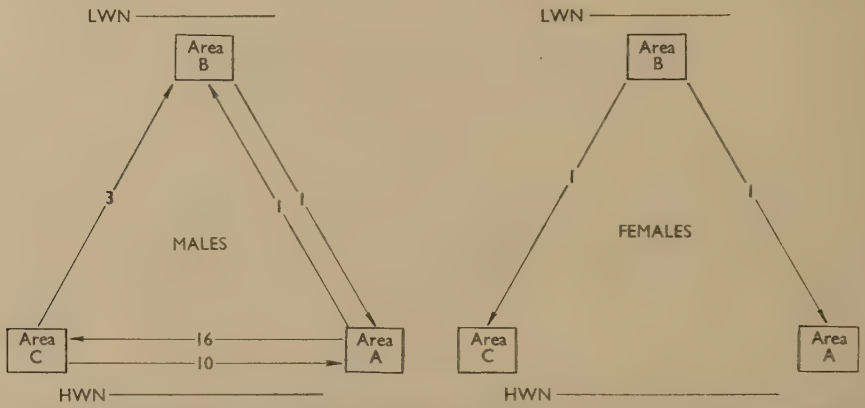


Fig. 2. The approximate relative positions of the three areas and the tide marks, with the numbers of males and females released in one area and recaptured in another.

females), of which 197 (171 males and 26 females) were recaptured at least once. Not only were more males captured but a much higher percentage of them were recaptured, 55% as against 22%. A total of thirty-three crabs (thirty-one males and two females) which had been released in one area were recaptured in another, and of these, two crabs, both males, subsequently reappeared in the area where they were originally released. These movements are shown graphically in Fig. 2. It is apparent that in the males there is far more interchange between A

and C than between either of these areas and area B. The two females which were recovered in a different area had both moved from area B to an on-shore area.

(*b*) *Population Estimates*

The data obtained from marking release and recapture were treated in the manner developed by Fisher & Ford (1947) and described in detail by Ford (1951).

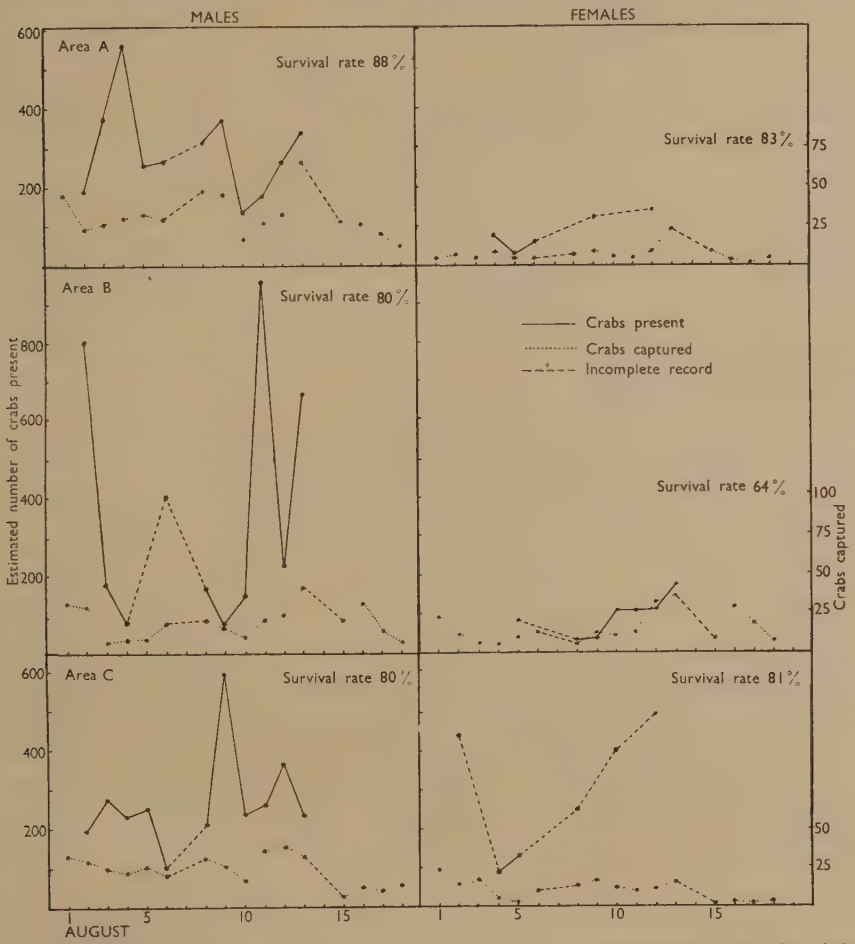


Fig. 3. The numbers of male and female crabs captured daily, and the estimated daily size of the populations in the three areas.

An estimate of the 'survival rate' is obtained by reducing to zero the discrepancy between the total days of survival observed, and that expected on the basis of an assumed survival rate. The size of the population on any given day is then estimated by a method which is a refinement of the Lincoln Index in which it is

assumed that if n marked animals are randomly distributed in a population of size N, the proportion of marked to unmarked animals in any subsequent sample will be n/N. In the experiments which Ford & Fisher carried out on butterfly populations it was known that interchange between the colonies was negligible and the 'survival rate' which they obtained was an indication of the length of life of the butterflies. In the present experiment the reverse is true, for the death rate during the experiment will be negligible and the 'survival rate' becomes a measure of the mean time the crabs spend in the particular area where they were marked and released.

The trellis diagrams showing captures, releases and recaptures are given in Table 1 and the estimated size of the population on any given day is shown graphically in Fig. 3, which also includes the number of crabs captured each day. Since the method of collection was the same on every occasion, changes in the numbers captured should reflect changes in the numbers present. That this is in general true can be seen by comparing the two curves. The population density expressed as number per unit area is much higher in area C than it is in either of the other areas. This may be due to the influence of the fresh-water stream which runs through it, for Broekhuysen (1936) has shown that *Carcinus* has a marked preference for water of low salinity.

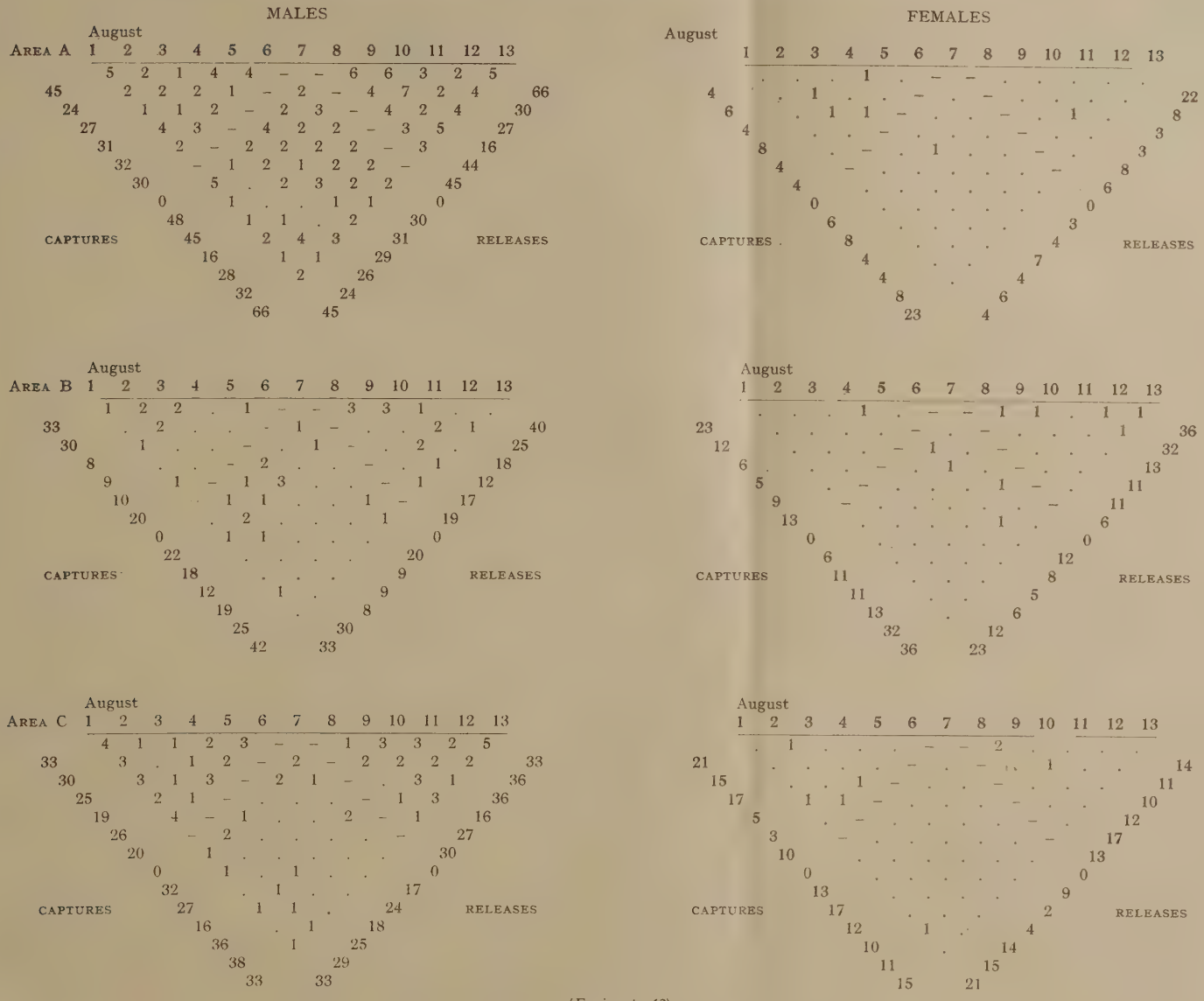
(*c*) *Measurements*

In the case of crabs collected on 15 to 18 August two measurements were taken, the carapace length (CL) and the distance between the teeth under the eyes (OW—see Fig. 1). These measurements had also been taken on crabs collected during preliminary investigations made on 13 and 14 April, 28 May, and 4 to 8 July.

The mean carapace lengths changed in all three areas during the periods of investigation (Fig. 4). In the male population of area B it was small in April, rose to a peak in May, then dropped again in August. In areas A and C it reached a peak in July and showed a similar drop in August. In the female population it was lower in May than in April, but then rose steadily and reached its peak in August. As all crabs with a carapace length of less than 30 mm have been rejected, the distribution of the measurements is not normal and the t test is inapplicable. The differences have therefore been subjected to the U test in which the distribution of the data is less critical (Mann & Whitney 1947). For males, these differences are significant at the 5% level between all periods in area B, and between April and all other periods in area A. For females the difference is significant only between May and August in area A. No other differences are significant.

A comparison of the mean carapace lengths of crabs taken from different areas shows that on each occasion males collected from area B were consistently larger than those taken from the other two areas, and that these differences are highly significant in all cases. On the other hand, there is no significant difference between males taken in areas A and C except in the case of those taken in August. In no instance is there any significant difference in the carapace length of females taken from different areas except between females taken from areas A and B in May.

Table 1. *Marking, release and recapture diagrams for males and females in the three areas*



(*Facing p. 42*)

The ratio of the measurements CL/OW (Fig. 1) was found to be less in the case of crabs taken from area B than in the case of those from either of the other areas, but since this ratio decreases with increasing carapace length the difference can be entirely accounted for by the larger size.

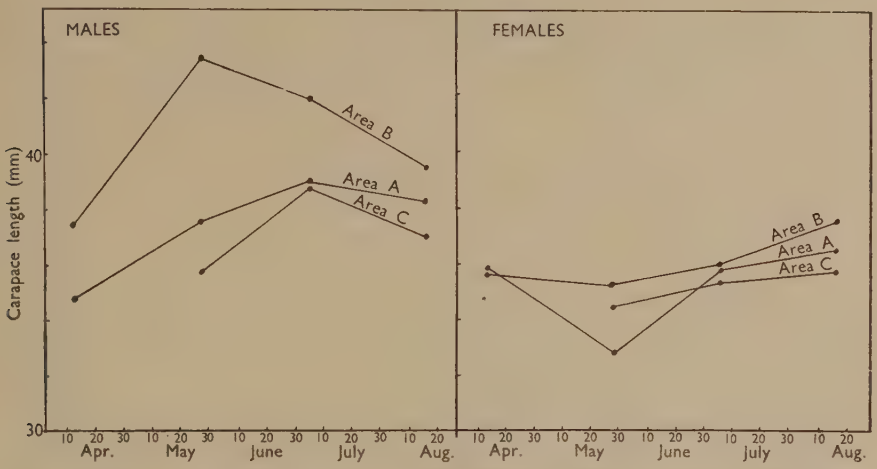


Fig. 4. Changes with time of the mean carapace length of male and female crabs in the three areas.

DISCUSSION

The results indicate such a marked difference in behaviour between the two sexes that they are best considered separately.

(*a*) *Males*

The most obvious feature of the male population is the violent daily fluctuation in estimated numbers. This is partly due to movements between the three areas, for the coefficients of variation of the areas considered separately are 51%, 93% and 55% whereas that for their sums is only 44%. But a coefficient of 44% is sufficiently high to suggest the existence of factors other than the normal sampling errors. A consideration of the survival rates and estimated size of the populations confirms that this is so. In area B, for example, the estimated mean population of 370 and the survival rate of 80% indicate that an average of 74 crabs leave the area every day. Since the population shows no marked downward trend there must be a corresponding immigration from some other source. The same is true of areas A and C in which there is a daily turnover of 36 and 55 respectively. As there is no other hiding place on the beach for hundreds of yards in each direction the only possible source from which these immigrants can have come is the sublittoral zone.

It is clear that on this shore there was a marked up and down movement of the population in which male crabs came in with the tide, remained for a short time, and then returned to the sublittoral zone. But the recaptures indicate that not all

the movement was of this type, for the number of crabs released in one of the two on-shore areas and subsequently found in the other is far greater than the number found in the off-shore area. Similarly very few crabs released in the off-shore area were subsequently found in the on-shore areas. Moreover, the recapture data show that a number of crabs were repeatedly captured in one or other of the on-shore areas at intervals throughout the experiment, and it is reasonable to suppose that they had remained there throughout. There is little doubt that whilst some crabs, probably the majority, remain in the sublittoral zone and make only occasional excursions up into the littoral zone, there are others which remain for periods of several days in the littoral zone, even as high as HWM. The difference in size between crabs found in area B on the one hand and in areas A and C on the other would be accounted for if the smaller crabs fall into this latter group.

(*b*) *Females*

The situation appears to be quite different in the case of the female population. Both the numbers captured and the estimated size of the population indicate that in all areas, and in areas B and C particularly, the numbers were high at the beginning of the month; they dropped sharply reaching a minimum in areas A and C on 5 August and in area B on 8 August; they increased to reach a peak in all three areas on 12 August; and then, judging from the number of captures, dropped again during the period 15 to 18 August to a very low level.

This sort of pattern would appear if there had been a gradual large-scale movement up and down the shore between HWM and the sublittoral zone but very little transverse movement. So far as it goes, the other evidence supports this assumption; there is no significant difference between the mean carapace lengths of the crabs in the three areas; the only two females known to have moved from one area to another had both travelled from area B to one of the on-shore areas and had been found there on 12 August; and the 'survival rate' of females in area B was particularly low, as would be expected if the crabs were moving rapidly through that area on their way to or from the sublittoral zone.

Since the numbers of females captured were so small, the apparent changes in the size of the population may be an illusion produced by sampling errors, but this is unlikely as it occurs at the same time in all three areas. The movement may have been part of some rhythmic behaviour pattern in which the whole female population undertakes a short-range migration at regular intervals, or may have been a casual movement brought about by some unusual factor. There was a period of high wind and rough seas during 3 to 5 August, and it is possible that this was sufficient to drive the females off the beach to seek shelter in deeper water, but if this were so, it is difficult to see why the males were not similarly affected, and why there should have been a drop in the number of females during 15 to 18 August when the weather was calm and very warm.

Although the evidence in the case of the females is too slender for any definite conclusions to be drawn, that for the males which is based on much larger numbers is more reliable. Some interesting information might have been obtained if the

sizes of all the crabs marked had been recorded, but unfortunately this could not be done as there was insufficient time to collect, mark and measure crabs taken from all three areas during the period of low tide.

ACKNOWLEDGMENTS

I wish to express my thanks to Dr E. B. Ford, from a discussion with whom the idea for this experiment arose, and to my wife, who helped me with the task of marking, measuring and recording the crabs.

SUMMARY

1. The method of marking, release and recapture was applied simultaneously for a period of two weeks to populations of crabs inhabiting three rocky areas on a sandy shore. Samples of crabs taken from all three areas were measured.

2. The 'survival rates' for males, indicated a daily immigration of 36 and 55 respectively into the two on-shore areas, and of 74 into the off-shore area. These crabs could only have come from the sublittoral zone.

3. Recaptures of marked males showed that there was much more interchange between the two on-shore areas than between either of these and the off-shore one.

4. Males taken from the off-shore area were consistently larger than those taken from either of the on-shore areas, but those from the on-shore areas did not differ significantly from each other.

5. It is concluded that there is a rapid up and down migration, in which the majority of the crabs take part, but that others remain mainly at the same level.

6. There was no significant difference between the mean sizes of the females in the three areas. Changes in numbers suggest that there were gradual movements of the whole population between the littoral and sublittoral zones. These may have been part of a rhythmic behaviour pattern or have been caused by some environmental factor such as rough seas.

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THRUSH PREDATION ON THE SNAIL *CEPAEA HORTENSIS*

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(With 2 Figures in the Text)

In the summer of 1953 Dr R. A. Hinde kindly drew my attention to the thrushes which were feeding on snails on the tops of bird cages at the Madingley Field Station, near Cambridge, and it seemed that this might provide an excellent opportunity for studying the effects of predation on a natural population of snails. I examined the cages on 29 June 1953 and collected 123 dead thrush-eaten shells of *Cepaea hortensis* (Müller) from their roofs. All dead shells were removed from the area, and regular collections were started in January 1954 and have been continued in an unbroken series at the end of every month for three years, until December 1956. Only shells with the upper part of the lip intact, where it joins the next whorl, were scored, so that the same shell could not be counted twice. The numbers of shells found in each month are shown in Fig. 1, and the different polymorphic shell types in Fig. 2 and Table 1.

All the shells were collected from a row of twenty cages, evenly spaced in a straight line for 140 yd along the eastern edge of a narrow strip of woodland, just inside the boundary fence of the Field Station. The cages were all the same, measuring 6 × 6 × 6 ft and made of wire netting on a steel frame. Each cage was partially roofed with a piece of asbestos sheeting, 6 × 2 ft in size, and it was these roofs that were being used by the thrushes as anvils for breaking open the snail shells. In the winter the shells were usually opened on the frozen ground close to the edges of the cages and an area extending 3 ft out around the bottom of each cage was also searched. The birds seemed to prefer to open the snails close to the cages and not many extra shells would have been found more than 3 ft from the cages. These well-defined and relatively small areas could be searched quite intensively, and a repeat search showed that very few of the shells in the specified area were being missed. The rest of the wood was carefully searched on several occasions, and some shells opened on tree-stumps well away from the cages were found, but it did appear that the cages were the main sites of the anvils used by the birds for opening snail shells. The only birds that were definitely seen feeding on snails were song thrushes, *Turdus ericetorum* Turton, but there were also missel thrushes, *T. viscivorus* L., in the wood and possibly other species as well in the winter. Apart from a few *Theba cantiana* (Mont.) the only thrush-eaten shells found were *Cepaea hortensis*; no *C. nemoralis* (L.) were found. The *C. hortensis* population in the wood did not appear to be a particularly abundant one. Practically all the shells seen on the anvils were fully grown or nearly so; younger snails may also be

eaten by thrushes but they evidently do not need to be broken open on an anvil. The wood was mixed deciduous, predominantly of elm trees, and during the autumn of 1955 some of the trees were cut out, making it considerably more open and with more vegetation on the ground during the following summer.

SEASONAL PREDATION

It can be seen from Fig. 1 that the snails are not taken at a constant rate throughout the year, but that there are two quite distinct periods of predation, when the

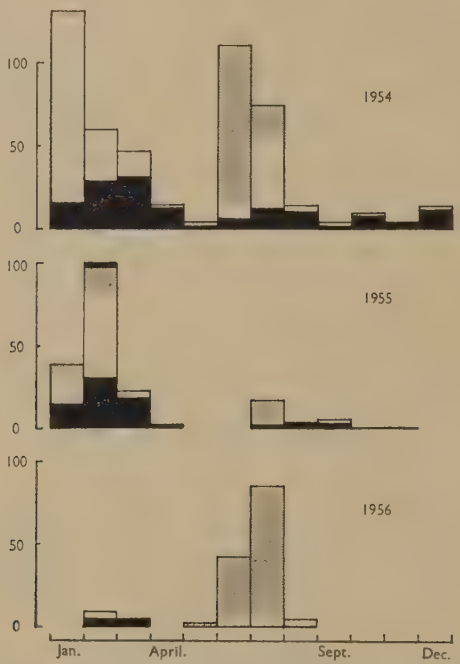

Fig. 1. Numbers of *Cepaea hortensis* killed by thrushes found at Madingley in each month of the years 1954-56. Shaded parts of the columns represent shells found on the cage tops; the rest were found on the ground within 3 ft of the cages. Old dead shells carried to the anvils by thrushes are shown black.

birds are feeding in the winter during January, February and March, and in the summer in June and July. Less than 10% of the total were taken during all the other months of the year. The summer feeding period was observed in each of the four consecutive summers from 1953 to 1956, and seems to correspond with the flying of the last brood of young thrushes. In 1954, for instance, a nest was seen close to the line of cages, and the young birds flew on about 15 June; it will be seen that only two freshly killed snails were found on 1 June, compared with 105 on 1 July. There was a poor catch in the summer of 1955, with no shells at all

found in June and only 17 in July, but the summer peak was clearly there and quite distinct though small. The spring of 1955 was warm and dry followed by cold wet weather at the end of May and in June, and it was a very late year for plants and insects, and also for birds, which nested later than usual. There were thrushes nesting in the wood near to the line of cages, but when they had finished nesting, in July, they must have had some other supply of food available. In September 1955 a number of trees were cut down in the wood, altering its character, but this was started too late for the disturbance to have affected the feeding habits of the thrushes during their usual snail-feeding period in June and July.

Similarly, in each of the three consecutive winters there was a distinct peak for predation in January or February, though it was a very low one in February 1956. These winter feeding periods are undoubtedly associated with hard frosty weather. The most snails for any one month were found in January 1954, which was generally cold with snow on the ground for much of the time. January 1955, however, was mild until the end of the month, and February, which was cold, produced many more predated snails. The poor catch in the winter of 1956 was, however, not due to mild weather, for there was a lot of frost in both February and March and *Cepaea hortensis* certainly was being eaten at that time; over 500 freshly killed snails were picked up along 100 yd of the verge of the road to Cambridge, half a mile from Madingley, in those two months. It may be that the disturbance of tree-felling the previous autumn had made the thrushes at Madingley move elsewhere for the whole winter, but the small catch during that winter cannot have been due to any lack of snails in the wood, as plenty were taken the following summer and they were mostly fully grown snails more than a year old, that must have been there during the preceding winter. There was further disturbance in the autumn of 1956, when most of the cages were moved and repainted, though not until after the end of the summer feeding period. Monthly searches were continued until December 1956 and no shells were found, as was to have been expected though the whole area had in any case been much disturbed.

Fig. 1 shows also that there was a systematic seasonal change in anvil sites. The shaded areas on the columns represent shells found on the asbestos sheeting cage roofs, but many of those found on the ground in the summer had probably been opened on top of the cages and fallen down. In the winter, on the other hand, most of the shells were found on the ground; there was only one on a cage top in the winter of 1954, 24 in 1955 compared with 138 on the ground, and none on the cage tops in 1956. In the winter the shells certainly were being opened on the ground by thrushes who used small stones, and blocks of ice that had been emptied out of the water dishes in the cages, as anvils. It is possible to tell from the way in which a shell has been opened whether a thrush or a rat is responsible (Morris 1954a), and none of the freshly killed snails found on the ground seemed to have been opened by rats. A possible explanation of the seasonal change in anvil sites may be that the birds choose sites in the open, away from cover for lurking predators. Thrushes opening snail shells are a familiar sight, and this suggests that there is at least no attempt at concealment. At Madingley the ground is bare in the winter but in the

summer it is overgrown with nettles and other vegetation, which may hide unseen dangers. The obvious explanation, that in the winter the ground is frozen hard so that shells can be opened anywhere while in the summer a hard surface is needed, is probably not correct, as stones or ice are needed as anvils in the winter and the stones at least are still available in the summer as well. Morris (1954a) also noted that thrushes did not seem to choose anvil sites offering cover, but that there was some evidence of choice in that snails were not opened close to an occupied nest.

Especially during the winter, an appreciable proportion of the shells found at the anvils were old empty ones, and these are shown black in Fig. 1. Some were intact empty shells but many had been opened by birds or rats. Only shells with their inner surfaces fresh and shiny were classified as fresh, the old shells being the ones with inner surfaces stained and weathered and usually with the whole shell weathered and long since dead. All the shells counted as old were without doubt empty when taken to the anvils, though some of those classified as fresh may have been opened elsewhere and also carried as empty shells to the anvils. Some of the old shells found on the ground within the area searched, especially during the first year, may not have been carried there by birds but have worked their way out of the soil, or been blown by the wind, but many of them certainly were carried by thrushes and were found scattered round the anvils together with freshly opened shells. Three of the shells found on cage tops in February 1955 were old ones, one of them empty but intact, and these must have been carried there by birds. Most of these old shells were quite obviously empty and it seems that a hungry bird in the winter searching the frozen ground for food may if it finds a snail shell, however obviously empty, often carry it to an anvil and go through the motions of hammering it before resuming the search. In the hard winter of 1954 about half the shells found at the anvils in February and March were old ones and there were a lot in the following winter as well, but in the summer few old shells were found, and none on the cage tops where most of the snails were being opened by the thrushes. Morris (1954b) also records seeing song thrushes 'on rare occasions' carrying empty shells and hammering them on anvils.

SELECTIVE PREDATION

Cepaea hortensis is a polymorphic species which shows a number of markedly different shell patterns and colours constituting its different 'morphs' (Huxley 1955). At Madingley there are two contrasting shell colours, yellow and pink, determined by a pair of allelomorphic genes, with pink dominant over yellow. There are also various different banding morphs based on the universally recessive pattern of five dark brown spiral bands running round the whorls of the shell, usually designated by the formula 12345. Any one or more of these bands may be fused with its neighbours, fusion being shown in the banding formulae by brackets, (12)345, 1(234)5, (123)(45) and so on, and it has been claimed (Boettger 1950) that these band fusion formulae in *C. hortensis* form an allelic series, with the greater band fusion dominant to the lesser. The 12345 pattern, with all the bands present

and none fused, is at any rate recessive to all the fusion formulae. At Madingley eleven different combinations of fused bands were found, as shown in Fig. 2, but since thrush-eaten shells often lack much of the first whorl, where the band fusion is best seen, there may be errors in the fusion patterns scored, giving an underestimate of the amount of fusion in the intact living snail. In addition, any one or more of the bands may be missing, this being shown by a zero in the formula, but the only ones found at Madingley were 00300 with a single central band, which was rare, and 00000 with no bands at all, which was the commonest single formula. The bandless 00000 pattern is allelomorphic with 12345 and shows linkage with the yellow – pink locus, and is dominant to all other patterns. The 00300 is probably dominant to everything except 00000, but there is evidence that its gene locus is on a different chromosome. In most colonies of *C. hortensis* (unlike the very similar sibling species *C. nemoralis*) the pink shell colour is commonly found only in bandless shells; that was so at Madingley, where out of a total collection of 960

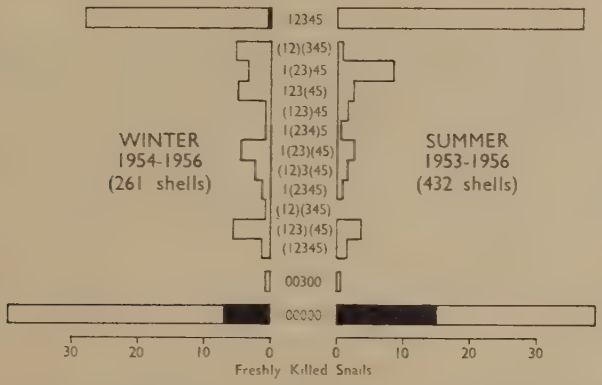

Fig. 2. Percentages of the different shell banding patterns in the aggregated total of predated shells found in four summers (June 1953, June and July 1954-56) compared with the total for four winters (January, February and March 1954-56) at Madingley. Pink shells are shown black; the rest are yellow.

shells 101 were bandless pinks and there was just one pink shell with bands. Another morph occurring at Madingley, though only eight shells were found, is the albino, in which the normally brown bands lack any pigment and are more or less transparent against the usual yellow background; this is recessive to the pigmented form. These few are shown under the appropriate banding formulae in Fig. 2, though at first sight they look more like unbanded 00000 shells. Illustrations of different banding patterns and references to work on their genetics are given in a previous paper (Goodhart 1956).

Sheppard (1951), working with the very similar *C. nemoralis*, showed that there was selective predation of the pink and yellow shells by thrushes at different seasons of the year. In two woods near Oxford, over a period of eight weeks in April

and May, the proportion of yellow shells found at thrushes' anvils progressively and significantly decreased. This was to be explained by the seasonal increase in green vegetation in the environment, against which yellow shells were less easily seen by visual predators than on the brown bare ground of early spring. Cain & Sheppard (1950, 1954) and Lamotte (1950) have suggested also that the shell banding pattern may be protective and help to conceal the snails on variegated backgrounds. At Madingley, where bird predation seems to be restricted to two distinct periods in the summer and winter, background differences and any effect of visual predation in maintaining the polymorphism should be maximal. It is interesting to find that there is some evidence of an effect of this kind, not very large but statistically highly significant. In Table 1 the collections made in the four summer and three winter feeding periods are analysed separately to show the main types of shell found, while Fig. 2 shows graphically all the different phenotypes represented in the summer and winter collections compared. Only freshly killed snails have been included in the figure since old shells are often faded and dis-

Table 1. *Numbers of dead* Cepaea hortensis *shells found around thrush anvils at Madingley at different periods of the year*

The figures have been analysed to show the different colours and banding patterns; freshly killed (fr) and old long dead (o) shells are shown separately.

	12345 (unfused)		12345 (fused)		00300		00000 (pink)		00000 (yellow)	
June and July	fr	o	fr	o	fr	o	fr	o	fr	o
1953	50	–	24	–	–	–	12	–	37	–
1954	63	8	43	5	1	–	19	2	41	4
1955	5	1	2	–	–	–	3	–	5	1
1956	40	–	37	–	1	–	29	–	20	–
January, February and March										
1954	46	25	44	21	–	2	14	7	59	20
1955	28	24	34	21	2	1	4	3	26	19
1956	–	3	2	2	–	–	–	2	2	3
All other months	10	18	8	21	1	2	2	4	5	22

coloured and may be less subject to differential visual predation, but the old shells are shown separately in the table and it can be seen that if they had been included the conclusions would have been the same. Table 1 shows that there is a preponderance of pink shells (all of them unbanded) in the summer collections; 14% of the total of the summer collections consisted of pink shells, compared with 7% for the winters, while in the summers 38% of the unbanded shells alone were pink, compared with 19% for the winter collections. A value of $\chi^2 = 9{\cdot}3134$ can be calculated for this difference in the proportion of pink shells in the aggregated totals of freshly killed snails in the summer compared with the winter collections, taken from the figures given in Table 1, which has a probability of less than 0·01 and so is highly significant; the thrushes really are finding about twice as many pink shells

in the summer as in the winter. It will be seen also that in the summer of 1956 the proportion of pink shells (22·8%) was distinctly higher than in the previous three summers, when it was 11·1%, and this difference also has a probability of less than 0·01. A possible explanation of this apparent increase in the selective disadvantage of pink shells in the summer of 1956 is that there was a good deal more green vegetation on the ground, as a result of the tree-felling the previous autumn, than in the previous years; according to Cain & Sheppard (1954) the pink shells should then become relatively more conspicuous to birds, and that does seem to have happened.

From Fig. 2 it is clear that there is no appreciable difference in the proportion of total banded compared with unbanded shells in winter and summer, about 39% being unbanded in each, but it looks as though there might be a slight excess of shells with fused bands in the winter. However, χ^2 tests for heterogeneity in fused bands in the six summer and winter collections, and also a 2×2 test on the summers and winters aggregated, give values that are well short of significance at the 5% level. There are no significant differences for any of the individual band fusion formulae.

These results therefore confirm Sheppard's observation that more pink shells are taken by birds in the summer than in the winter when the ground is bare, though there is no evidence at Madingley of any differential predation of shell banding patterns. Schnetter & Sedlmair (1953) and Sedlmair (1956) have shown that the pink and yellow varieties of *Cepaea hortensis*, and also of *C. nemoralis*, behave differently under similar conditions of temperature and humidity. Thus for *C. hortensis* the optimum temperature, as measured in a multiple choice apparatus, was 20° C for yellow unbanded snails, compared with 17° C for the yellow banded form, and in *C. nemoralis* the optimum for pink shells was 14° C as compared with 20° C for yellow. Under bright, dry and warm conditions unbanded *C. nemoralis* were more active than the banded forms, but less so when it was dark, damp and cold. In *C. hortensis* the unbanded yellow forms were more active than banded in dry conditions after light adaptation, but less so after dark adaptation. The situation is obviously a complicated one, and it is said that the relative activity of different forms from the same locality under similar conditions differs from year to year, presumably depending upon the weather. Boettger (1954) also has reported finding differential resistance to bright light and high temperature in *C. hortensis*, yellow bandless shells being the most resistant to these conditions. It must anyhow be accepted that there is evidence that the different genotypes do not all react in the same way to environmental conditions. If that is so, visual selection of the different shell patterns and colours is not necessarily the only possible explanation of the observed seasonal changes in the proportions of the different phenotypes taken by thrushes. No doubt a snail crawling about actively has a greater risk of being found by a bird than one lying withdrawn into its shell and hidden in the undergrowth, irrespective of its colour. If, therefore, the different shell types show differential activity, that could explain seasonal changes in predation rates. However, as it appears that the yellow and unbanded snails are the more active under

warm dry conditions it is to be expected that their risk should be greater in the summer than in the winter or spring, which is contrary to what was found at Madingley, and also by Sheppard (1951) for *C. nemoralis*. At Madingley all the snails taken by thrushes during the winter feeding period must have been entirely inactive, hibernating and buried in the soil or under dead leaves, and so the sample collected by the thrushes was probably an unbiased one reflecting the true composition of the whole population. There is, of course, the possibility that different genotypes might behave differently when hibernating; if pink-shelled snails buried themselves deeper in the soil they would be harder to find and that would produce a bias in the sample collected by the birds. On balance, however, it seems more likely that seasonal changes in the proportions of different phenotypes collected by birds are due to differential visual selection by the predators, rather than to differential behaviour of the prey.

DISCUSSION

It is clear that the population of *Cepaea hortensis* at Madingley really is subjected to two quite distinct and widely separated periods of predation by thrushes in the summer and winter, with very few snails taken in between. This has been observed quite regularly, though varying in extent, over three years and more. A seasonal change in anvil sites has been noted, but it can hardly be supposed that in the off seasons the thrushes should have been eating snails but opening them at some different lot of anvils, that have not been found despite several intensive searches throughout the wood. This does not, however, necessarily mean that all populations of this snail should show similar effects of seasonal predation. Sheppard (1951) working with two colonies of *C. nemoralis* in woods near Oxford in 1950 found that thrushes were taking the snails during the second half of April and throughout May, although at Madingley there was an almost complete cessation of thrush predation during these two months. *C. nemoralis* is very similar to *C. hortensis* and it is not likely that the differences in predation should be due to specific differences between the snails, especially as the same species of thrush, *Turdus ericetorum*, was the predator in both cases.

It is well known that thrushes feed on snails in hard weather. Collet (1927, p. 262) speaks of snails being used as an 'emergency ration' in hard frosts and suggests also that they are taken as well 'during July droughts when the soil is equally impenetrable'. The observations at Madingley confirm this, at least so far as hard weather in the winter is concerned, and snails do not seem to be taken by thrushes during the winter except when the ground is frozen hard. This may suggest that, as very often happens with 'emergency rations', the thrushes do not find snails particularly palatable as food. Hibernating snails are no more difficult to find in November and December or when the ground is not frozen than when it is frozen hard in January, February and March, and yet they are not taken then by birds. That suggests that there may be other and preferable foods available at those times, worms and insects perhaps, and the thrushes turn to snails only when these

alternative foods can no longer be found in really cold weather. Hartley (1954a) found that fieldfares (*Turdus pilaris* L.) fed on crab apples only during the hardest weather in the winter, using them as an 'ecological reserve' of food when there was nothing else to be had. It seems that the song thrush uses snails in the same way as an ecological reserve in the winter.

At Madingley the thrushes do not begin feeding on snails in the summer until June, and that cannot simply be because there are more birds about then after the new generation is fledged. Myres (1955) found that nearly 70% of the song thrush clutches in a large sample from the south of England over four years were started before the end of April, and about 25% in March, so the fledglings from these clutches should be quite independent and able to feed on snails before June. At Madingley the summer feeding period only started towards the end of June and it seemed to be correlated with the flying of the last broods of thrushes, not the earlier ones. It looks as though it is the parent birds, when they have finally finished their parental duties, rather than the newly fledged young, who start this summer feeding period. This again may not necessarily be the typical state of affairs, for Morris (1954a) found parent thrushes taking snails while the young were still in the nest, although more were taken after it had been abandoned, and Hartley (1954b) saw snails being fed to newly fledged young thrushes by their parents. The suggestion that snails are taken in the summer only when the ground is hard during a drought cannot, however, be accepted; at Madingley the ground in the wood is seldom really hard and dry, and June and July 1954 when there was a big catch of snails were not particularly dry months. August, September and October are generally the dry months in Cambridge, but very few snails are taken then.

It has been argued that in the winter thrushes feed on *Cepaea hortensis* only during hard frosts *faute de mieux*, but that they prefer other kinds of food if they are available, and it seems likely that the rather restricted summer feeding period may be due to similar causes. The snails are certainly freely available crawling about after damp weather throughout the summer from April until October, and yet they are only taken by thrushes in June and July. They may well not be a suitable food for nestlings, but it is rather surprising that they are not eaten by the parent birds in the spring when they are not feeding nestlings, and even more surprising that they are not taken in the late summer and autumn when there are no nestlings to be fed, and plenty of snails about. But if *C. hortensis* is not a thrush's first choice as food, it may be eaten in June and July only because there is some temporary shortage of other food at this time, when the bird population is at its highest, and perhaps between an abundant supply of insect larvae in the spring and the fruits of the later summer and autumn. Snails are then eaten as a second choice as they are in the other period of food shortage in frosty winter weather. Thrushes have a varied diet and the particular foods that they eat at any one time or place may be the result of a nice balance between availability and palatability, so the discrepancy found between the feeding periods at Madingley and those in the Oxford colonies studies by Sheppard need cause no surprise. The small catch of

snails in the summer of 1955 at Madingley may be the result of similar effects, for the weather was unusual that year and the early caterpillar season may well have been postponed into June and July, when food in a normal year is short and thrushes usually have to add snails to their diet.

From the point of view of the snails this pattern of restricted and widely separated seasonal periods of predation, whatever its causes, will accentuate any effect of differential selective predation in maintaining what may be called 'predation polymorphism' in the population. If pink shells are relatively more likely to be taken by predators in the summer than in the winter, the absence of bird predation in the spring and autumn will make sharper the distinction between any seasonal risks run by the different genotypes. This seems to be what happens at Madingley, but it need not be so in all colonies, even those living in apparently rather similar habitats; elsewhere there may be predation during the spring, which will tend to blur its effect in maintaining the polymorphism. The situation is, of course, a very complex one and differential predation can be only one among many of the factors concerned. In *Cepaea* there are so many different shell patterns and colours involved in the polymorphism that no visual predator could distinguish between them all, and different genotypes certainly do have different effects upon activity and hardiness, and also probably upon viability, fertility, ageing and other physiological processes, all of which must be factors of importance in natural selection.

SUMMARY

1. Shells of *Cepaea hortensis* eaten by song thrushes were collected from the same area every month for three years.

2. The birds fed on snails only during two restricted periods of the year, in January, February and March, and in June and July, with hardly any taken in between. *C. hortensis* is probably not very palatable as food to thrushes and serves as an ecological reserve, being taken only when other food is short during cold weather in the winter, and in mid-summer after the spring flush of caterpillars and before there is much fruit available.

3. During the winter feeding period quite a high proportion of dead empty shells were taken by thrushes to their anvils.

4. There was evidence of a systematic seasonal change in the anvil sites.

5. Significantly more pink than yellow shells were taken by thrushes in the summer than in the winter feeding periods, but no differential predation of the various shell banding patterns could be observed. Various possible reasons for this differential predation are discussed, and it is concluded that visual selection by birds, rather than genetic differences in activity in the snails, provides the best explanation. This could be responsible for maintaining some 'predation polymorphism' in the species, but the situation is a complex one and there are certainly other factors involved as well.

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FACTORS INFLUENCING THE STAPLE FOOD OF TSETSE FLIES

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(With 1 Figure in the Text)

Collections of smears of gut contents prepared from a number of different species of tsetse (*Glossina*) over a wide area ranging from the Sudan to Southern Rhodesia (Weitz & Glasgow 1956) all indicated that the family Suidae (represented by only two species, warthog and bushpig) was the most important constituent of the diet of tsetse of the *morsitans* group (*G. morsitans*, *swynnertoni*, *pallidipes* and *austeni*). This conclusion was accepted with reserve, because the method used to collect the recently fed tsetse did not exclude the possibility of serious bias. They were collected from the flies attracted to moving parties of two or three men (see the description of 'fly-rounds' given by Buxton 1955, p. 444). No gorged females are captured by this method, and the collection of males is not satisfactory, since only about 1% of the males captured are found to contain identifiable blood. It is known that tsetse feed every three to six days, according to season (Jackson 1954), and that the blood remains identifiable for 24 h after ingestion (Weitz & Buxton 1953). A fair sample of a tsetse population would therefore be expected to include 16% or more of individuals containing identifiable blood, but this is never achieved in catches from moving objects. This is not surprising, because attraction to moving objects is part of the tsetse's host-finding mechanism. Recently fed tsetse do not, in general, respond to moving objects. Males investigate moving objects before they become hungry; this reaction brings the sexes together and ensures fertilization of the females even at very low population densities. Thus it is clear that gorged tsetse which are captured on fly-rounds are rare and exceptional. They include no females, because in this sex, attraction to moving objects is confined to the hungriest individuals, and the number of males with identifiable blood is unrepresentative. It seemed possible that such males might be atypical not only in behaviour but also in respect of (and perhaps because of) the kind of blood they contained, and it also seemed possible that the diet of the sexes could differ.

One of us (Isherwood 1957) described the collection of *G. swynnertoni* Austen from its resting sites. Many such tsetse, including numerous females, contain recognizable blood. We decided to examine collections of gorged flies made in one place at intervals throughout a year, with the object of ascertaining whether the

diet of males and females is the same, whether samples of males collected by the new resting technique gave the same results as samples collected by the old fly round technique, and whether any changes of host associated with season or age could be detected.

PROCEDURES

The feeds were identified by the precipitin test for groups of species of hosts, and by the inhibition test for individual species (Weitz 1956). The validity of the results obtained by these methods was discussed by Weitz & Glasgow (1956). During the present investigation further checks were made in August, October and December by the inclusion of control blood smears derived from captive tsetse artificially fed on known animals, including man, monkey, warthog, bushpig, reedbuck, steinbok and porcupine. These control smears were forwarded to the laboratory for testing, without notice, as part of the larger samples of wild feeds. The bulk of the controls were correctly identified. No errors occurred among the identifications of Suidae, although of eight warthog feeds only three were identified specifically as warthog, one as unidentified Suidae and four as unidentified mammal. Three feeds were identified as giraffe and one as eland, although they were derived from reedbuck and steinbok. This error was due to the use of an unsuitable antiserum which fortunately was not used for the unknown flies and would thus not affect the results obtained. As the proportion of Suidae identified specifically among the unknown flies was much greater than that of the controls, we conclude that the nature of the two groups of smears was different. It is noteworthy that no Suidae smears were identified as anything else, and that no other feeds were identified as Suidae. This result is very important in view of the prominence assumed by warthog in the results given below.

This investigation was conducted in an area of thorn-bush known as Block 9 in Shinyanga in the Lake Province of Tanganyika. It is nearly 50 sq. miles in extent, and surrounded by open country, the Sukumaland cultivation steppe, on all sides. Game is completely protected, but an occasional lion or rhinoceros ventures out of the block and has to be shot. An unknown number of warthog and bushpig are destroyed by neighbouring cultivators. Other possible hosts of tsetse are kudu, eland, roan antelope, reedbuck, Thomson's gazelle, duiker, dikdik, impala, steinbok, giraffe, baboon, monkey, elephant, mongoose and birds. Warthog and impala are the commonest animals. Unfortunately it is not at present possible to say anything more about the true or relative abundance of these various animals, nor whether the habits of any of them put them into especially close or remote contact with tsetse. Studies of these matters are projected. In Block 9 *Glossina swynnertoni* Austen is abundant, with an apparent density* of the order of 100. *G. pallidipes* Austen has an A.D. of the order of 1. We planned to collect a

* Apparent density, or A.D., signifies the number of non-teneral males captured on a fly-round of the standard length of 10 000 yd. Teneral tsetse are defined as those which have not yet had their first meal; they are recognized by their feel and appearance.

sample of about a hundred resting recently fed *G. swynnertoni* of each sex each month. For comparison, we collected about a hundred recently fed active male *G. swynnertoni*. It was not possible to collect a sample of recently fed active female *G. swynnertoni*, because this class scarcely exists. After a time it was found possible to collect recently fed resting *G. pallidipes*, whereupon a sample of these was added to the monthly collection. From the time taken to collect the monthly samples we judged that *G. pallidipes* was about half as numerous as *G. swynnertoni*, although as noted above the fly-round data suggested the ratio was about one to a hundred. This is an example of differential availability of tsetse species: *G. pallidipes* is very little attracted to man, so that relatively dense populations yield very small catches on fly-rounds.

The recently fed flies were brought into the laboratory where the gut contents were expressed on to clean filter paper and stored in desiccators until the end of the month when they were forwarded to the Lister Institute. The wings of each tsetse were mounted, the cutting edge of the hatchet cell measured, and the wing assigned to a fray category, as in Jackson (1946). The measurement of the wing gives a rough idea of the size of the fly. The mean length varied seasonally in the now familiar way described by Jackson (1953), and will not be considered further here. The data on fray gives information on the mean age of the sample from which it is derived. This varied in a remarkable manner which will be described later.

DISCUSSION OF RESULTS

After five months we decided that the results were so regular that the sampling frequency could be reduced to once every other month without losing much information. Thus we have samples from February to June inclusive, and from August, October and December. These results are summarized in Tables 1-3. It is clear that 'Total Suidae' is of overwhelming importance in all groups, warthog being the more important, with bushpig a very poor second.

Fig. 1 shows the total Suidae as a percentage in each of the five different collections month by month. It is clear that *G. swynnertoni* females take a higher proportion of Suidae feeds than do males, and that in most months a higher proportion of Suidae feeds is observed in resting males than in active males. Though the difference between male and female resting *G. swynnertoni* is not large, it is statistically significant, because if they were the same, the chances of the difference (males – females) having the same sign on each of eight occasions is given by the expansion of $(1/2+1/2)^8$, *i.e.* 2/256 or 0·008 (Fisher 1944). In the same way the proportion of Suidae feeds is significantly higher in *G. pallidipes* than in *G. swynnertoni*, but our figures do not demonstrate any difference between the sexes of this species. Comparing the Suidae feeds observed in active and resting male *G. swynnertoni*, the proportion is not significantly higher in resting males in any one month, but if the four months May, June, August and October are combined, the proportion of Suidae is significantly higher by χ^2 in resting males, P being 0·02-0·01. Before discussing possible reasons for these differences, the difference in age

Table 1. *Results of identification of the blood meals of* G. swynnertoni *resting males and females—1956*

MALES	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Number of feeds identified	105	112	83	143	113	0	98	0	124	0	165	943
Hosts:												
Warthog	74	91	64	101	76	0	62	0	90	0	124	
Bushpig	4	0	0	0	2	0	0	0	0	0	3	
Unidentified Suidae	8	1	6	16	13	0	16	0	5	0	6	
Total Suidae	86	92	70	117	91	0	78	0	95	0	133	762 (81%)
Kudu	6	1	1	4	1	0	5	0	0	0	5	
Eland	0	0	0	0	0	0	3	0	1	0	8	
Kudu or Eland	0	0	0	0	0	0	1	0	2	0	1	
Roan antelope	1	0	0	0	3	0	0	0	0	0	1	
Duiker	1	0	0	0	0	0	0	0	0	0	0	
Impala	0	0	1	2	1	0	0	0	3	0	1	
Giraffe	4	1	1	3	3	0	1	0	8	0	6	
Unidentified ruminants	0	0	0	1	2	0	7	0	1	0	1	
Total ruminants	12	2	3	10	10	0	17	0	15	0	23	92 (10%)
Man	6	8	4	6	9	0	0	0	7	0	2	
Baboon	0	0	0	1	0	0	0	0	0	0	0	
Monkey	0	1	0	1	0	0	0	0	0	0	0	
Unidentified Primates	1	0	0	3	0	0	0	0	0	0	0	
Total Primates	7	9	4	11	9	0	0	0	7	0	2	49 (5%)
Rhinoceros	0	7	4	5	1	0	3	0	5	0	7	
Elephant	0	0	0	0	0	0	0	0	0	0	0	
Dog	0	0	0	0	0	0	0	0	0	0	0	
Cat	0	0	0	0	0	0	0	0	0	0	0	
Unidentified mammals	0	2	2	0	2	0	0	0	2	0	0	
Total other mammals	0	9	6	5	3	0	3	0	7	0	7	40 (4%)
Birds	0	0	0	0	0	0	0	0	0	0	0	

FEMALES	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Number of feeds identified	104	96	120	104	100	0	69	0	95	0	129	817
Hosts:												
Warthog	70	86	104	84	79	0	54	0	74	0	103	
Bushpig	6	2	0	0	0	0	1	0	0	0	3	
Unidentified Suidae	14	4	9	7	9	0	4	0	7	0	8	
Total Suidae	90	92	113	91	88	0	59	0	81	0	114	728 (89%)
Kudu	2	0	0	0	1	0	5	0	0	0	0	
Eland	0	0	0	0	0	0	1	0	0	0	7	
Kudu or Eland	0	0	0	0	0	0	0	0	0	0	1	
Roan antelope	0	0	0	1	2	0	1	0	1	0	0	
Thomson's gazelle	1	0	0	0	0	0	0	0	0	0	0	
Impala	0	0	0	1	0	0	0	0	0	0	0	
Giraffe	0	0	0	0	2	0	1	0	8	0	3	
Unidentified ruminants	0	0	0	0	1	0	2	0	1	0	2	
Total ruminants	3	0	0	2	6	0	10	0	10	0	13	44 (5%)

Man	5	3	1	4	5	0	0	0	1	0	0	
Baboon	0	0	0	0	0	0	0	0	0	0	0	
Monkey	0	0	0	0	0	0	0	0	0	0	0	
Unidentified Primates	1	0	1	1	0	0	0	0	0	0	0	
Total Primates	6	3	2	5	5	0	0	0	1	0	0	22 (3%)
Rhinoceros	4	0	0	3	1	0	0	0	3	0	2	
Elephant	0	0	0	1	0	0	0	0	0	0	0	
Dog	0	0	0	0	0	0	0	0	0	0	0	
Cat	0	0	0	0	0	0	0	0	0	0	0	
Unidentified mammals	1	1	5	2	0	0	0	0	0	0	0	
Total other mammals	5	1	5	6	1	0	0	0	3	0	2	23 (3%)
Birds	0	0	0	0	0	0	0	0	0	0	0	

Table 2. *Results of identification of the blood meals of* G. swynnertoni *active males—1956*

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Number of feeds identified	114	97	111	86	116	0	104	0	108	0	110	846
Hosts:												
Warthog	64	79	79	42	70	0	57	0	72	0	78	
Bushpig	3	1	3	0	1	0	0	0	1	0	7	
Unidentified Suidae	8	0	10	21	16	0	19	0	1	0	16	
Total Suidae	75	80	92	63	87	0	76	0	74	0	101	648 (77%)
Kudu	6	2	0	0	4	0	1	0	0	0	1	
Eland	3	0	2	0	0	0	0	0	2	0	0	
Kudu or Eland	0	0	0	5	0	0	0	0	1	0	0	
Roan antelope	1	0	0	5	3	0	2	0	4	0	1	
Reedbuck	1	0	0	0	0	0	0	0	0	0	0	
Duiker	0	0	0	0	0	0	2	0	0	0	0	
Impala	0	0	0	1	1	0	0	0	4	0	0	
Giraffe	6	1	4	1	1	0	1	0	8	0	3	
Unidentified ruminants	10	1	0	0	3	0	1	0	3	0	1	
Total ruminants	27	4	6	12	12	0	7	0	22	0	6	96 (11%)
Man	3	5	5	3	5	0	0	0	0	0	0	
Baboon	0	0	0	0	0	0	0	0	0	0	0	
Monkey	0	1	0	0	0	0	0	0	0	0	0	
Unidentified Primates	3	0	2	0	0	0	1	0	0	0	0	
Total Primates	6	6	7	3	5	0	1	0	0	0	0	28 (4%)
Rhinoceros	5	6	1	5	4	0	12	0	11	0	1	
Elephant	0	0	0	0	0	0	0	0	0	0	0	
Dog	0	0	0	0	0	0	0	0	0	0	1	
Cat	0	1	0	0	0	0	0	0	0	0	0	
Unidentified mammals	1	0	5	3	8	0	5	0	1	0	1	
Total other mammals	6	7	6	8	12	0	17	0	12	0	3	71 (8%)
Birds	0	0	0	0	0	0	3	0	0	0	0	3 (0·4%)

between the samples of active and resting males should be noted, again from Fig. 1. The active males are always older than the resting males, except in the height of the dry season. The following explanation is proposed for the curious age difference between the active and the resting sample.

Table 3. *Results of identification of the blood meals of resting* G. pallidipes — *1956*

MALES	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Number of feeds identified	0	7	24	0	40	0	75	0	48	0	77	271
Hosts:												
Warthog	0	7	22	0	31	0	59	0	42	0	62	
Bushpig	0	0	0	0	1	0	0	0	0	0	2	
Unidentified Suidae	0	0	2	0	5	0	11	0	5	0	8	
Total Suidae	0	7	24	0	37	0	70	0	47	0	72	257 (95%)
Kudu	0	0	0	0	1	0	1	0	0	0	2	
Eland	0	0	0	0	0	0	1	0	0	0	0	
Kudu or Eland	0	0	0	0	0	0	0	0	1	0	0	
Roan antelope	0	0	0	0	0	0	1	0	0	0	1	
Giraffe	0	0	0	0	0	0	0	0	0	0	0	
Unidentified ruminants	0	0	0	0	0	0	0	0	0	0	1	
Total ruminants	0	0	0	0	1	0	3	0	1	0	4	9 (3%)
Rhinoceros	0	0	0	0	0	0	0	0	0	0	1	
Mongoose	0	0	0	0	0	0	1	0	0	0	0	
Unidentified mammals	0	0	0	0	2	0	1	0	0	0	0	
Total other mammals	0	0	0	0	2	0	2	0	0	0	1	5 (2%)

FEMALES	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Number of feeds identified	0	0	21	3	57	0	55	0	36	0	48	220
Hosts:												
Warthog	0	0	16	3	46	0	46	0	30	0	44	
Bushpig	0	0	0	0	0	0	0	0	0	0	0	
Unidentified Suidae	0	0	3	0	7	0	2	0	5	0	3	
Total Suidae	0	0	19	3	53	0	48	0	35	0	47	205 (93%)
Kudu	0	0	0	0	1	0	4	0	0	0	0	
Eland	0	0	0	0	0	0	1	0	0	0	0	
Kudu or Eland	0	0	0	0	0	0	0	0	0	0	0	
Roan antelope	0	0	0	0	1	0	1	0	0	0	1	
Giraffe	0	0	0	0	1	0	1	0	1	0	0	
Unidentified ruminants	0	0	1	0	0	0	0	0	0	0	0	
Total ruminants	0	0	1	0	3	0	7	0	1	0	1	13 (6%)
Rhinoceros	0	0	1	0	1	0	0	0	0	0	0	
Mongoose	0	0	0	0	0	0	0	0	0	0	0	
Unidentified mammals	0	0	0	0	0	0	0	0	0	0	0	
Total other mammals	0	0	1	0	1	0	0	0	0	0	0	2 (1%)

After feeding, a male tsetse proceeds to a suitable tree where it rests and digests. After a time, when it has greatly reduced the weight of its meal by excreting excess water (Buxton 1955, p. 81), and also, as we believe, made some progress

with the process of digestion, if it is a mature male it becomes responsive to moving objects, to which it is attracted although not yet in need of food. If it still contains identifiable blood, then after it leaves its perch it becomes liable to capture and inclusion in our 'active' sample, whereas before it left its perch it would, if discovered, be included in our 'resting' sample. In the case of *G. palpalis* R.-D. it is known that males in captivity take more than eight days to become fully virile (Nash 1955). If wild *G. swynnertoni* behave similarly it is easy to imagine

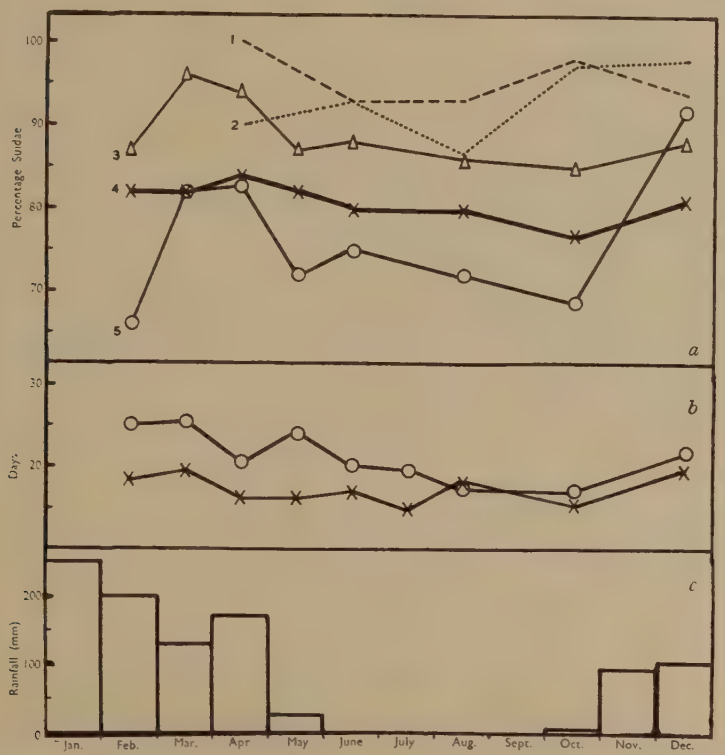

Fig. 1. *a*, the percentage of feeds on Suidae in each of the five collections month by month: 1, *Glossina pallidipes* females; 2, *G. pallidipes* males; 3, *G. swynnertoni* resting females; 4, *G. swynnertoni* resting males; 5, *G. swynnertoni* active males.
b, the age in days of male *G. swynnertoni*; O——O, active; X——X, resting.
c, monthly rainfall in mm.

that flies less than a certain critical age do not leave their resting places until digestion has gone so far that they no longer contain identifiable blood. In this case, the 'active' sample must consist only of flies above this critical age, and the 'resting' sample would tend to be deficient in elderly flies which had gone off to join the 'active' sample. It remains to explain how this age difference disappears in the dry season. It appears from Fig. 1 that in this season the 'active' flies are younger than in any other. It is known that this season the mean life of males may

be as little as two weeks (Jackson 1949) and we suppose that while life is very short the age difference between 'resting' and 'active' samples cannot be manifested.

To explain the consistently higher level of 'Total Suidae' meals taken by female *G. swynnertoni* we find it necessary to postulate that Suidae are preferred. Then we may suppose that a time comes in the female hunger cycle when the female will leave her resting place and feed if she perceives a preferred host, but not for any other reason. Later on, if a preferred host has not offered itself, she gets desperately hungry and will then take anything she can find. Males, however, get to the stage of responding to non-Suidae earlier, and though they may not be hungry when they first respond, doubtless flight makes them hungry and having reached the non-preferred host we may suppose that some take a meal before leaving it. The lower proportion of 'Total Suidae' taken by active males can be explained on a similar basis, if we are right in presuming that the more elderly 'active' males on the whole leave their resting places earlier in their hunger cycle than do the younger 'resting' males. To explain the higher proportion of 'Total Suidae' feeds taken by *G. pallidipes* we can only suggest that its preference for them is stronger than that of *G. swynnertoni*. As it is certain that *G. pallidipes* has a stronger distaste for man than *G. swynnertoni* has, the other proposition is not incredible.

There is an apparent tendency for more 'Total Suidae' feeds to be taken in March and April. We are not sure that the peak in the 'active' males curve is real because at about this time we suspected that the fly-boys, realizing that it was easier to get resting than active flies containing blood, possibly misreported the source of some of the flies. No such doubt is entertained about the peak in active males in December. A general increase in the proportion of feeds from a preferred host would be understandable in the rains when the hunger cycle is longest, but as the graph shows the increase was not general. The peak in resting females in March is not suspect at all, but we are unable to suggest an explanation for it which would not require a corresponding peak in the resting males.

SOME INCIDENTAL COLLECTIONS

On 9 February 1956 thirty-six gorged *G. swynnertoni* were collected in an area covered with giraffe spoor. They were part of the 'resting' sample for February, but are mentioned here because at the time we supposed they might all prove to be giraffe. The actual determinations are given in Table 4. On 6 and 9 April 1956, sixty-six gorged flies were taken in a thicket containing an inhabited warthog burrow. These we expected to find had all fed on warthog, but as shown in Table 4, the proportion of warthog was little greater than that general in April. These two examples are of interest in demonstrating how little weight can be given to anecdotes describing the discovery of gorged tsetse in association with traces of some potential host.

Some gorged males were captured on routine fly-rounds which embrace a much larger area than the rather restricted neighbourhood of the Mwakilendya river, where the bulk of the collections considered in this paper were made. During 1956

Table 4. *Results of identification of blood meals of* Glossina swynnertoni *and* G. pallidipes *associated with giraffe and warthog*

Figures give numbers observed and percentages in parentheses.

	Flies associated with giraffe spoor – Feb. 1956		Flies associated with warthog – April 1956			
	G. swynnertoni		*G. swynnertoni*		*G. pallidipes*	
	males	females	males	females	males	females
Number identified	28 (100)	11 (100)	13 (100)	26 (100)	16 (100)	12 (100)
Hosts:						
Warthog	17 (60)	11 (100)	12 (93)	21 (81)	16 (100)	12 (100)
Bushpig	1 (4)	0	0	0	0	0
Unidentified Suidae	2 (7)	0	0	1 (4)	0	0
Total Suidae	20 (71)	11 (100)	12 (93)	22 (85)	16 (100)	12 (100)
Kudu	1 (4)	0	1 (7)	0	0	0
Giraffe	3 (11)	0	0	0	0	0
Unidentified ruminant	1 (4)	0	0	1 (4)	0	0
Total ruminants	5 (18)	0	1 (7)	1 (4)	0	0
Man	3 (11)	0	0	1 (4)	0	0
Unidentified Primate	0	0	0	1 (4)	0	0
,, mammal	0	0	0	1 (4)	0	0
Total Suidae in the month for comparison	– (82)	– (87)	– (84)	– (93)	– (100)	– (95)

Table 5. *Identification of blood meals of* G. morsitans *in the Singida district—September-October 1956*

	Ulyampiti	Ntua and Lindi
Number identified	54	103
Hosts:		
Warthog	0	5
Bushpig	1	1
Unidentified Suidae	2	2
Total Suidae	3 (6%)	8 (8%)
Kudu	30	4
Eland	3	1
Eland or Kudu	0	8
Reedbuck	0	1
Ox	1	0
Ox or buffalo	1	0
Buffalo	0	27
Giraffe	0	4
Unidentified ruminants	4	25
Total ruminants	39 (72%)	70 (68%)
Rhinoceros	3	17
Man	9	3
Unidentified mammals	0	5

the proportion of total Suidae in the fly-round collection was 83% (79/95) and in the closely comparable 'active males' 76% (648/846), suggesting that the Mwakilendya area was not specially favoured by pigs.

In September 1956 a collection of blood meals from *G. morsitans* in Ulyampiti in the Singida district of Tanganyika was made. The identifications of these meals are given in Table 5. Ulyampiti is an area where *Brachystegia* woodland, inhabited by *Glossina morsitans*, interdigitates with the vegetation type known as 'Itigi thicket', which is not inhabited by *G. morsitans* but is used by such bush-loving animals as kudu and rhinoceros. Although warthog and bushpig occur at Ulyampiti, Table 5 shows that here they are of minor importance to *G. morsitans*. A month later a larger collection was made in the Ntua and Lindi areas, a few miles north of Ulyampiti and less intimately associated with Itigi thicket. The results of this collection are also given in Table 5. It is clear that in the one area kudu has the sort

Table 6. *The identification of blood meals of* G. morsitans *in two areas with and without hippopotamus—1956*

Kamalia		Mburo and Ruemondo	
Warthog	26	Warthog	9
Unidentified Suidae	2		
Total Suidae	28 (67%)	Total Suidae	9 (20%)
Buffalo	3	Buffalo	9
Bushbuck	1	Eland	6
Total ruminants	4	Bushbuck	1
		Bushbuck or Eland	2
		Waterbuck	1
		Unidentified ruminants	4
		Total ruminants	23
Dog	1	Hippopotamus	11
Man	2	Unidentified mammals	1
Unidentified mammals	7		
Total	42	Total	44

of importance that warthog has in Shinyanga, and in the other, buffalo. These observations are included here because the general trend of the rest of this paper, and of the previous paper (Weitz & Glasgow 1956) might lead one to suppose that Suidae are always and everywhere the most important host of *G. morsitans* and *G. swynnertoni*, which are very similar and closely related. The Singida results show that under natural conditions more than one species of Bovidae can on occasion replace the Suidae as the chief host. Another example gives in Table 6 the results of two collections of gorged *G. morsitans* from the Ankole district of Uganda. The two places are only 20 miles apart. Kamalia has no hippopotamus and perhaps no eland. Mburo is near the lake of that name, which contains the hippopotamus. The striking differences between the two places are presumed to be bound up with differential host availability.

In the same way it will be recalled from the earlier paper that *G. pallidipes* from two adjacent areas was found to be feeding in one case on bushpig and in the other

on bushbuck. In Shinyanga, although kudu (a close relative of bushbuck) and bushpig are present, warthog is overwhelmingly the most important food. Unless the preference of one species of tsetse varies markedly from place to place, the answer to these anomalies must lie in the habits of the host animals, about which very little information is at present available. Further collections from these areas will be made to check the regularity of such anomalies.

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SUMMARY

1. Collections of gorged *Glossina swynnertoni* and *G. pallidipes* were made by two methods at Shinyanga throughout a year, and the gut contents identified serologically.

2. In all months Suidae were the most important group of hosts. Active male *G. swynnertoni* (the group corresponding to all previous collections) averaged about 76% Suidae; resting males about 80%, resting females about 90%, and both sexes of *G. pallidipes* about 94%.

3. Although the collections considered in previous work (Weitz & Glasgow 1956) were biased because they consisted of smears from active males only, it is now shown that the conclusions reached are applicable to the population of tsetse as a whole.

4. To explain the differences between the various collections it seems necessary to postulate that tsetse exercise a definite preference for Suidae.

5. Nevertheless, areas are known where kudu, buffalo or hippopotamus appear to be more important than Suidae to *G. morsitans*.

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A CAPTURE-RECAPTURE ANALYSIS OF A SHEARWATER POPULATION

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WITH A STATISTICAL APPENDIX

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Since Lincoln (1930) estimated the total number of waterfowl in North America by noting the proportion of marked individuals shot during the hunting season, the use of recapture data has become one of the best-known methods for analysing animal populations. Jackson (1933) independently used the same method for estimating the density of tsetse flies (*Glossina morsitans*) and further expanded the theory (1937, 1939, 1940, 1948) with his negative and positive methods to allow for the complications introduced by birth- and death-rates and migration. The method was applied to Lepidoptera populations by Dowdeswell, Fisher & Ford (1940, 1949) and to the sheep blowfly (*Lucilia cuprina*) by Gilmour, Waterhouse & McIntyre (1946). Bailey (1951) was the first to consider the precision of such estimates and also provided a convenient summary of the literature (Bailey 1952).

The only detailed analysis by the capture-recapture method of a wild bird population is that of Hammersley (1953) using data on the Alpine Swift (*Apus melba*) obtained for quite another purpose by H. Arn. It was found that the birds were not captured at random and the fundamental assumption of the capture-recapture method was therefore not satisfied, but the analysis was continued to illustrate the possible applications of the technique. Hammersley stressed that because the sampling was not random great care must be taken when interpreting the results of his analysis.

In an important series of papers (Leslie & Chitty 1951, Leslie 1952, and Leslie, Chitty & Chitty 1953) an elaborate mathematical treatment of the estimates of death-rate and total numbers was developed and the methods applied to free-living populations of voles (*Microtus agrestis* and *Clethrionomys glareolus*). *Clethrionomys* was apparently sampled at random, but in the case of *Microtus* the unmarked animals were not. However, by using only the data from marked *Microtus*, which were found to have been randomly sampled, estimates of the death-rates were made.

Leslie & Chitty (1951) were also the first to analyse the important bearing of the method of grouping the information upon the ease of the calculations and the precision of the estimates.

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Let $r_{012\ldots t}$ = the number of individuals recaptured at time t having been previously caught and marked at 0, 1, 2, ... $(t-1)$. In most sampling experiments the size of the sample and the number of recaptures are likely to be small relative to the total population at risk. Therefore, a set of frequency distributions of $r_{012\ldots t}$ would consist largely of small numbers, and the number of possible classes of marks becomes very large as the length of the chain increases. In order to simplify the calculations some method of grouping the observations is adopted, ideally one which simplifies the equations and minimizes the loss of information. Leslie & Chitty showed that the method of grouping employed by Jackson & Dowdeswell *et al.*, in which each individual is counted as many times as it has been recaptured, simplifies the equations but results in a loss of information. They further showed that this loss increases as the size of the sample and the number of recaptures forms a larger proportion of the total population being sampled.

The present paper gives the results of an analysis of the population of Manx shearwaters (*Procellaria puffinus*) breeding on Skokholm Island, Pembrokeshire. Here too the material was gathered for an entirely different purpose, namely to determine the migration and winter range of the species, but because of the vast amount of information gathered, and because the supposition of random sampling seemed plausible, an analysis seemed profitable. Because marked individuals formed a large proportion of the captures, particularly in later years, grouping the results according to marks would have resulted in a substantial loss of information. Therefore, the method adopted in this analysis was Method B, as defined by Leslie & Chitty (1951), which results in the individuals being grouped according to the time they were last captured. For the full mathematical development of this method and a discussion of its precision the reader is referred to the three papers by Leslie & Chitty mentioned above.

THE SHEARWATER POPULATION

Shearwaters have been intensively studied on Skokholm during the breeding season by Lockley (1930, 1931, 1935, 1953) and by Matthews (1953, 1954). The birds are common on the island by the end of February but the single egg is not laid until between 25 April and 20 May. Both sexes share incubation, taking irregular shifts which average five days but are longer during moonlight periods. The birds return to the island only at night throughout the breeding season and as there are no marked fluctuations in the number of birds returning, except in full-moon periods, it can be assumed that individual pairs change over independent of their neighbours. There seems to be considerable competition for good burrows. Many nest failures are due to disturbance from other pairs of shearwaters and also rabbits which use the same burrows. Intruders visit some of the burrows much of the season. The number of burrows opened for the first time which contained no egg, increased from 13% in the period 10 May to 6 June, to 25% in the period 7 June to 6 July. Part of this increase may be due to immature birds arriving at the island later in the season than the breeding adults. Intermittent breeding as a regular

phenomenon seems unlikely in view of the many instances of known consecutive breeding. Destruction of eggs as a result of fighting and intrusion by other shearwaters seems to be the most likely explanation.

Between 17 June and 12 July 90% of the hatchings occur after an average incubation period of 53 days. The young are brooded for the first week and then left alone, the parents returning at night to feed them. When approximately two months old the young are deserted completely by their parents and after about a fortnight they half-run, half-fly to the sea.

With the exception of the war years shearwaters have been studied continuously at Skokholm since 1928. Ringing was begun in 1929 but not on a large scale until 1935. Since the war over two thousand individuals have been ringed annually (Table 1). Ringing is done mainly at night by groups of people with torches

Table 1. *Numbers of shearwaters ringed at Skokholm*

Totals do not include new rings used to replace worn-out ones.

	Adults	Nestlings	Total
1946	1440	12	1452
1947	2583	1308	3891
1948	3587	2252	5839
1949	2145	1049	3194
1950	1800	561	2361
1951	2110	693	2803
1952	2652	631	3283
1953	2297	689	2986
1954	3113	785	3898
			29 707

wandering over certain sections of the island picking up the birds sitting on the ground. Some birds are also ringed from accessible burrows. Towards the end of the season, when the young come to the entrances of the burrows, they are caught in large numbers. Large numbers of previously ringed shearwaters are picked up during these nocturnal excursions. In all cases the ring numbers have been carefully noted and the ring replaced if it showed signs of wear. Rings used in the first years were so weak that they seldom lasted longer than two years. Since then the quality of rings has greatly improved, but even now, in spite of a few which have lasted much longer, they are known to fall off after five or six years of contact with rocks and salt water.

Although birds are ringed on Skokholm from April to September, all birds caught in a given year are considered, for the purpose of analysis, to have been ringed on the same day. This has been necessary not only for convenience of grouping the information, but also because it was not noted when birds were captured more than once in a given season. This results in neglecting the deaths during the sampling period, but it is hoped that the error which this introduces into the estimates is not significant. Because of the poor quality of the earlier rings, the smaller numbers of birds ringed, and the war interruption, the pre-war data were

found unsuitable for this type of analysis. The following calculations are based upon ringing from 1946-53 and recaptures from 1947-54. Full details have been deposited in the Edward Grey Institute, Oxford.

RECOVERIES OF BIRDS RINGED AS NESTLINGS

Nestlings are apparently indistinguishable from adults once they have lost their down, so that while it is known that 6 of the 1308 nestlings ringed in 1947 were captured in 1948, there is no way of knowing how many unringed 1947 nestlings were caught. Since this must be known for a capture-recapture analysis, the recaptures of nestlings have been instead grouped separately (Table 2) from the

Table 2. *Recoveries of nestlings*

Year ringed	Number ringed	Years of recapture						
		1948	1949	1950	1951	1952	1953	1954
1946	12	–	–	–	–	1	–	–
1947	1308	6	10	23	9	8	2	1
1948	2252		7	8	20	32	10	5
1949	1049			8	2	8	10	–
1950	561				2	5	6	16
1951	693					1	1	19
1952	631						2	6
1953	689							–

time they were first captured (Method C, Leslie & Chitty 1951). These recaptures follow the same pattern in all years. They are low the first year, rise during subsequent years, reach a peak in the third or fourth year after ringing, and then drop off rather suddenly. However, the number of individuals alive decreases from the first year onward. Lockley believed that shearwaters did not breed until they were at least two years of age, but Table 2 strongly suggests that most juveniles do not return to Skokholm until they are at least three or four years of age, and it is quite likely that they do not breed their first year back on the island.

Unfortunately few data are available on the age at which Tubinares first breed. As regards species of small size, Richdale (1949) recovered three non-breeding diving petrels (*Pelecanoides urinctrix*) in burrows their first season after fledging, and seven including those three were found breeding in the following year when all reared chicks (Richdale 1952). Gross (1947) recovered two non-breeding first-year Leach's petrels (*Oceanodroma leucorrhoa*) and he found one breeding in its third year. In the sooty shearwater (*Procellaria grisea*), a medium-sized species perhaps comparable with the Manx shearwater, Richdale (1952) recovered an individual in its fifth year with a ring so fresh in comparison with those of breeding birds that he concluded that the ring had not been in contact with soil and rock before that year. In a large species, the Royal Albatross (*Diomeda epomophora*), six young birds returned to the breeding colony before they were of breeding age, one in its fourth year, one in its sixth, one in its seventh, and three in their eighth year, whereas a

seven-year-old female and an eight-year-old female did not breed at those ages (Richdale 1952). This information suggests that four or five years is not an unreasonable age for Manx shearwaters to breed for the first time. Furthermore, we might expect individual variation as has been found in many other species (Lack 1954, p. 63). It also supports the view that the birds return to the island at least one year before breeding. This explanation would in part account for the large number of birds found occupying burrows which laid no egg (Lockley 1942, Matthews 1953).

Since, as will be shown later, the mortality rate in shearwaters must be very low, the rather sharp drop in the number of recoveries in the fifth and subsequent years requires explanation. It would seem that two factors are responsible for this. The loss of rings may be considerable by the fifth year as the birds begin to spend a great deal of time on land where ring wear is greater. Also, if large numbers of birds are returning to the island in their third and fourth years but are not breeding the first year of their return, they would be expected to spend a greater portion of time on the surface of the ground and thus at high risk of recapture than in subsequent years, when they were breeding and spending most of their time in their burrows or at sea, in either case at low risk of recapture. Further detailed work on the island is necessary to test these tentative conclusions.

PRELIMINARY ANALYSIS OF ADULT RECAPTURES

The recaptures of all shearwaters ringed as adults, that is when at least one year of age, are grouped in Table 3 from the year last captured (Method B, Leslie & Chitty 1951). A preliminary analysis was first made by a method similar to that used by Leslie, Chitty & Chitty (1953) for voles.

Table 3. *Shearwater ringing recoveries—adults*

Year last captured	Years of recapture								
	1946	1947	1948	1949	1950	1951	1952	1953	1954
1946	–	189	82	51	42	22	17	7	2
1947	–	–	405	172	95	56	47	14	1
1948	–	–	–	474	232	149	128	62	20
1949	–	–	–	–	413	146	88	55	43
1950	–	–	–	–	–	314	174	98	78
1951	–	–	–	–	–	–	285	133	121
1952	–	–	–	–	–	–	–	276	256
1953	–	–	–	–	–	–	–	–	428
Total already ringed	–	189	487	697	782	687	739	645	949
Total unringed	1440	2583	3587	2145	1800	1720	2167	1908	2667
Total catch	1440	2772	4074	2842	2582	2407	2906	2553	3616

For the purpose of analysis let the population consist of N_t individuals at time t.

Let P = the constant survival factor, so that out of N_t individuals alive at time t, PN_t will be alive at time $t+1$;

and m_{xt} = the number of individuals captured at time t which were last captured at time x ($x = 0, 1, 2, \ldots, (t-1)$).

From Table 3 a new table was formed by retaining each $m_{t-1,t}$ entry and then summing each column of m_{xt} over the values of $x = 0$ to $x = t-2$.
Thus for each value of t greater than one there are a pair of observed values

$$m_{t-1,t} \text{ and } n_t = \sum_{t=0}^{t-2} m_{xt}$$

S_t was then calculated by adding together $m_{t-1,t}$ and n_t, *i.e.* S_t equals the total marked catch.

From these entries and the number of animals captured, C_t, together with the value

$$y_t = C_t - S_t \text{ (}i.e.\ y_t = \text{the unmarked catch at time } t\text{)}$$

the maximum likelihood estimate was calculated

$$\hat{\psi}\, t = \frac{n_{t+1} C_t}{m_{t,\,t+1}} + S_t \quad (t = 0, 1, 2, \ldots, T-1)$$

and then the survival factor

$$P_t = \frac{\hat{\psi}_{t+1}}{\hat{\psi}_t + y_t} \qquad (t = 0, 1, 2, \ldots, T-2)$$

and the total population size

$$N_t = \hat{\psi}_t \frac{C_t}{S_t}.$$

Table 4. *Preliminary analysis of adult recoveries*

	t	P_t	N_t
0	1946	–	–
1	1947	·754	11 000
2	1948	·540	20 086
3	1949	·715	13 197
4	1950	·800	12 709
5	1951	·741	15 840
6	1952	·553	18 183
7	1953	–	14 855

The results of the application of this method to the data contained in Table 3 are shown in Table 4 where the figures are entered opposite the year in which the sample was taken.

(*a*) *Population Size*

In 1929 Lockley (1930) by determining the number of burrows per acre estimated the breeding population of shearwaters on Skokholm at between 9000 and 10 000 birds. Later he revised his estimate to 20 000 breeding birds (Lockley 1942) but apparently without giving his reasons. The estimates obtained by the present preliminary analysis are not at variance with Lockley's estimates, but since, as will be shown in succeeding sections of this paper, the sampling upon which these estimates are based is non-random, they are subject to an unknown degree of bias.

(b) Death-rate

The calculations of a yearly survival-rate between 54 and 80% seemed low and this was tested by two other estimates. Dr G. V. T. Matthews kindly placed at my disposal the recapture information which he obtained while using shearwaters in his homing experiments during 1951-54. In these years 759 burrows were equipped with observation shafts and careful records kept. Since the object of this work was to recover birds which had homed, and since he wished to use the same birds for several years, a definite search was made for the birds in the observation area. The sampling is thus likely to be highly non-random, but since only birds proved to be breeding were used and because the rate of recovery was high, the minimum survival-rate can be extracted and the probable value of the actual survival-rate estimated from this. It should be noted that birds recaptured by Matthews were not included in Table 3.

Table 5. *Recoveries of shearwaters during homing experiments*

Data from G. V. T. Matthews, 1951-54;
percentages of original totals are given in parentheses.

A. Recoveries of mature birds found with eggs or young in year of ringing

	Total ringed	Recovered in burrow area		
		in next year	two years later	three years later
1951	213	97 (45%)	76 (36%)	65 (30%)
1952	394	182 (46%)	123 (31%)	–
1953	318	123 (39%)	–	–

B. Table 5A modified by including all birds known to be alive

	Total ringed	Still alive after		
		one year	two years	three years
1951	213	156 (73%)	99 (46%)	66 (31%)
1952	394	216 (55%)	129 (33%)	–
1953	318	127 (40%)	–	–

C. Reoccupation of burrows

	Burrows dug	Intact and occupied for breeding		
		in next year	two years later	three years later
1951	190	106 (56%)	83 (44%)	51 (27%)
1952	233	135 (58%)	55 (24%)	–
1953	163	98 (60%)	–	–

In Table 5A the recaptures of shearwaters dug from their burrows in the observation area are shown. For each year the total number of birds ringed and the number recovered in subsequent years are given. The percentages of the original number ringed are included in parentheses. Thus of 213 birds ringed in 1951 97 or 45% were recovered in the burrows in 1952, and 76 or 36% in 1953, and 65 or 30% in 1954.

While only 97 of 213 birds ringed in 1951 were recovered in the burrows the following year, many more were known to be alive as an additional 59 were subsequently recaptured, chiefly on other parts of the island. Therefore, Table 5A has

been amended (Table 5B) to include all birds known to be alive at that time by virtue of their being recovered either during that year or in subsequent years. By adding to the 97 individuals recovered from the observation burrows the 59 individuals recovered elsewhere, the known survival-rate in the first year of the 213 birds ringed in 1951 has been raised to 73%. The corresponding figures for birds ringed in 1952 and 1953 are as yet much lower because there has been only one or no later years in which to catch additional birds.

The high loss during the first year after ringing in Table 5A is unexpected since this sample consisted entirely of breeding adults of varying, but unknown, age and there is no reason to expect the actual mortality to be higher the first year. It is likely that the destruction of burrows is the chief factor causing high loss during the first year. After one year about one-fifth of the burrows disappeared for one reason or another and another one-fifth, although remaining intact, were not inhabited. The opening of inspection shafts, despite precautions, undoubtedly caused greater than normal destruction of burrows by increasing their exposure to weather. Table 5C shows the number of burrows still intact and occupied. If a bird whose burrow is destroyed is unable to locate another near by, it is likely to nest outside the area of observed holes where its chances of being recovered are much lower. Furthermore disturbance may cause the birds to shift though the burrow still remains intact. If the 20% of birds whose burrows have collapsed are nesting elsewhere the actual survival-rate would be of the order of 90%.

Because of the great yearly variations in the number of shearwaters reported as shot by fishermen in the Bay of Biscay, the source of most foreign recoveries, the analysis of these records provided no reliable estimates of the survival-rate, but another estimate was obtained by considering the probable reproductive success of the species. Only 50% of the eggs produced mature chicks in the colony studied by Lockley (1942). If we take it that with an equal sex ratio each breeding female lays one egg and there is a 50% mortality in the nest; and that a female starts laying in the fourth year following her birth; and finally that once out of the nest all the individuals are immortal; then the annual rate of increase (λ) of the population would be given by the real positive root of the equation

$$\lambda^4 - \lambda^3 - 0{\cdot}25 = 0$$

from which we have $\lambda = 1{\cdot}16$. In other words the population would multiply 1·16 times every year. Therefore, if the population were stationary in numbers, the probability of surviving for a year, averaged over all age-groups in the population, cannot be less than $P = 0{\cdot}84$.

But shearwaters are not immortal after leaving their burrows, and in fact we would expect mortality to be highest among the first-year birds (Lack 1946), so that we are again led to believe that adult shearwaters survive at a rate higher than 90% per year. However, the preliminary estimates of survival values calculated from the capture-recapture data are much lower. This strongly suggests a large error due to the sampling having been non-random. The data were therefore further analysed to check this point and to determine, if possible, the nature of the bias.

TESTS FOR RANDOM SAMPLING

As a first step in the analysis of the sampling, a new table of adult recaptures (Table 6) was formed. To do this the raw data were treated in a manner very similar to that used to form Table 3, except that individuals which were captured only once were considered to form the unmarked population, the first recapture

Table 6. *Ringing recoveries of adults once recaptured*

	Years of re-recapture							
Year last captured	1947	1948	1949	1950	1951	1952	1953	1954
1947	–	45	14	5	6	3	3	0
1948	–	–	89	37	11	10	3	0
1949	–	–	–	118	41	24	10	5
1950	–	–	–	–	137	57	24	12
1951	–	–	–	–	–	104	32	27
1952	–	–	–	–	–	–	91	73
1953	–	–	–	–	–	–	–	112
Total already ringed	–	45	103	160	195	198	163	229
Total unringed	116	282	419	430	363	432	399	719
Total catch	116	327	522	590	558	630	562	948

was treated as the original marking, the second recapture as the first recapture, etc. By disregarding all birds which were not recaptured at least once the amount of data is considerably reduced, but this sub-population can be used to estimate a known parameter against which we can compare our calculated estimates. This parameter is

Z_t = the number of new birds added to the marked population at the sampling time t.

Table 7. *Preliminary analysis—adults once recaptured*

	t	Z_t (calculated)	Z_t (true)
0	1947	–	–
1	1948	1210	3587
2	1949	1148	2145
3	1950	885	1800
4	1951	1451	1720
5	1952	1701	2167
6	1953	2163	1908

Using the same symbols as in the previous section, Table 7 can be constructed from Table 6 and the estimates of Z obtained by the formula

$$Z_t = R_t \frac{(S_t C_{t+1} - n_{t+1} C_t - 1)}{S_t m_{t,t+1}} \quad (t = 1, 2, 3, \ldots, T-1)$$

The mathematical development of this test is given in the appendix to Leslie, Chitty & Chitty (1953). In the present analysis $R_t = C_t$.

The true values of Z_t are taken directly from Table 3 and compared with the estimates of Z_t calculated from the re-recapture data. The marked discrepancy

between the figures is at once apparent, again indicating that the sampling of the marked population was not at random.

A further proof of non-random sampling was obtained by analysing the recapture frequency of groups of known individuals. For example twenty-two birds ringed as adults for the first time in 1947 were recaptured for the last time in 1953. In the intervening years each of these individuals had the opportunity to be captured 0, 1, 2, 3, 4, or 5 times. By tabulating the frequency distribution of recaptures and the years of recapture a χ^2 analysis can be performed to determine whether these individuals, known to be alive during the intervening years, were actually recaptured at random (see the statistical appendix to this paper by P. H. Leslie). This type of analysis was performed for all yearly intervals. To make each calcula-

Table 8. *Chi- squared tests for random sampling*

Interval	χ^2	Degrees of freedom	Normal deviate with unit variance $\sqrt{2\chi^2} - \sqrt{2\,\text{d.f.} - 1}$
1946-53	40·83	29	
1946-52	50·32	31	
1946-51	33·35	25	
1946-50	104·59	60	
Total	229·09	145	4·40
1947-53	20·66	21	
1947-52	102·99	64	
1947-51	102·16	59	
Total	225·81	144	4·31
1948-54	71·28	59	
1948-53	101·39	80	
1948-52	183·71	155	
Total	356·38	294	2·47
1949-54	87·02	70	
1949-53	106·26	73	
Total	193·28	143	2·78

tion independent of the others, no individual was used in more than one estimate. In other words a bird ringed in 1947 and recaptured both in 1952 and 1953 was included in the analysis of sampling during the interval 1947-53 but not in the 1947-52 interval. The values of χ^2 for each interval, together with the degrees of freedom and the normal deviate with unit variance, are given in Table 8. These results show that the sampling of marked shearwaters had been highly non-random.

While the analysis of recapture frequencies shows that the sampling was non-random, it offers no clues to the nature of the bias. To examine this tables of the recaptures of adults released in 1947, 1948 and 1949, grouped according to the time they were last recaptured, were formed (Table 9). Since in this case a known group of individuals is considered, there is no dilution occurring, and the variable death-rate is the only factor operating. The total numbers of these individuals surviving

in the successive years after their initial ringing can be estimated by a method given by Leslie (1952, p. 379) where a numerical example of the details of the calculations are found. Having estimated the number of survivors in the successive years, we can then easily determine $P_t = N_{t+1}/N_t$. It is the last column of the table, the survival-rate, which is of greatest interest in this case. In all three groups there is

Table 9. *History of the adult shearwaters released in 1947, 1948 and 1949*

Year last captured	Years of recapture							Estimated numbers	Survival factor
	1948	1949	1950	1951	1952	1953	1954		
2772 adults released in 1947									
1948	–	67	26	9	6	2	–	1338	·48
1949	–	–	34	7	8	–	–	1179	·88
1950	–	–	–	18	7	1	–	799	·68
1951	–	–	–	–	8	3	5	437	·55
1952	–	–	–	–	–	5	8	186	·43
1953	–	–	–	–	–	–	2	125	·67
Total already ringed	–	67	60	34	29	11	15		
Total unringed	337	153	82	42	40	11	1		
Total catch	337	220	142	76	69	22	16		
4074 adults released in 1948									
1949	–	–	72	28	17	6	7	1914	·47
1950	–	–	–	42	23	8	2	1625	·85
1951	–	–	–	–	27	7	7	1505	·93
1952	–	–	–	–	–	17	10	972	·65
1953	–	–	–	–	–	–	16	363	·37
Total already ringed	–	–	72	70	67	38	42		
Total unringed	–	386	194	136	119	60	20		
Total catch	–	386	266	206	186	98	62		
2842 adults released in 1949									
1950	–	–	–	67	23	14	8	896	·32
1951	–	–	–	–	29	5	8	875	·97
1952	–	–	–	–	–	15	7	702	·80
1953	–	–	–	–	–	–	6	769	1·10
Total already ringed	–	–	–	67	52	34	29		
Total unringed	–	–	291	97	64	44	39		
Total catch	–	–	291	164	116	78	68		

an apparent low survival during the first year after ringing, a high survival in the two succeeding years, and a subsequent drop to very low survival after four or five years. Since, however, the birds of these samples were all adults of varying but unknown age, we should expect the survival-rate to be approximately constant over these years and not to exhibit such remarkable fluctuations. The drop in survival-rate after several years is almost certainly due to the loss of rings through abrasion. The apparent low survival during the first year after ringing is more difficult to explain. Since dozens of different people, both experienced and inexperienced, have placed rings upon the birds, it is possible that some of them are put on so poorly that they come off quickly during the first year, but it is doubtful whether this is a sufficient explanation as most rings were placed by the Warden or

Assistant Warden. Birds after being captured, handled and ringed, might be less inclined to return to the same breeding colony or might spend less time on the surface of the ground, but the results of Matthews's homing work indicate that it is unlikely that the birds are greatly disturbed by handling, at least not enough to cause many of them to desert eggs or young or to change breeding localities in subsequent years.

If, as is likely, birds return to the island at least one year before beginning to breed and spend a considerable amount of time during that year sitting on the surface of the ground at high risk of capture, a substantial proportion of 'adults' ringed in any given year may consist of such birds. They would be breeding the year following their first capture and consequently spending far more time either at sea or beneath the surface of the ground so that few would be taken, causing an apparent high mortality. Once, however, this breeding pattern is adopted by the sexually mature adults, a constant proportion of them should be taken until the loss of rings again imposes an apparent mortality. This would mean that, once breeding, the birds were actually sampled at random and therefore more significance could be attached to the maximum survival-rates of 88, 93 and 97% shown in Table 9. A further breakdown of the data was attempted to test this but the numbers of recaptures were then too small to analyse properly.

Attractive though this hypothesis is, it does not take into account the large numbers of birds, about 50% of the breeding population, which lose their eggs or young and leave the island. Since sampling continues from April to September, successful breeding adults that are returning to the island regularly throughout this period have a greater chance of being captured than individuals that lose their eggs in May and might be expected to return to the island less frequently after that. At the present stage of the development of the capture-recapture method it is impossible to say in what manner and to what extent this alters the analysis used in this paper. The hypothesis of visitation to the island the year before breeding, and the maximum survival-rates in the second and third year after ringing of 88, 93 and 97% fit well with the results expected by a consideration of the biology of the species and of the returns of birds used in homing work. Nevertheless, the possible effects of non-random sampling on the estimates cannot at present be calculated, so that great caution is necessary.

THE USE AND MISUSE OF THE CAPTURE-RECAPTURE METHOD

Because the sampling of the shearwater population did not fulfil the random requirement of the capture-recapture method of population analysis, it was impossible to arrive at trustworthy estimates of either the death-rate or the total size of the population. Nevertheless, the analysis indicates the most likely sources of error in the sampling methods so that future ringing on Skokholm, designed to alleviate them, could yield reliable estimates. The results which can be obtained from adequate sampling will well repay the time spent in planning. When used with proper caution the capture-recapture method can be one of the most useful statistical tools available to the biologist, but this analysis of a shearwater popula-

tion stresses the importance of first determining whether the data conform to the assumptions of the method. It also illustrates several means by which this can be tested and emphasizes the need for proper design of the sampling methods so that the maximum amount of information can be obtained from the field data.

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SUMMARY

1. The breeding population of Manx shearwaters on Skokholm Island, Pembrokeshire, was analysed by the capture-recapture method.

2. The recoveries of birds ringed as nestlings showed that most of them do not return to the island until they are three or four years old. The loss of rings causes an apparent high mortality in later years.

3. Preliminary estimates of the survival-rate of shearwaters ringed as adults were between 50 and 80% but a consideration of the probable reproductive success of the species and the recoveries of birds used in homing experiments indicated that the survival-rate must be above 90% per year.

4. Further testing showed that the sampling was highly non-random, the nature of the bias suggesting that most birds visited the island at least one year before breeding, at which time they were more easily caught than later, when they spent less time on the surface of the ground. This view explains the high loss the first year after ringing, after which the survival-rates rose to 88, 93 and 97% in the second or third years.

5. The capture-recapture method can be a valuable tool for the biologist if sampling experiments are carefully designed and if care is taken to determine whether the sampling conforms to the assumptions of the theory.

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STATISTICAL APPENDIX

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When a large number of birds are ringed and recovered in the subsequent samples from a population, a way of testing whether the ringed birds were being sampled at random is the following.

Suppose that Z_t birds were ringed for the first time and released in some particular year t. Then, in following the individual histories of the members of this group, a certain number of them—say, N_{s+1}—will have been last recovered at the $(s+1)^{\text{th}}$ sampling following the date of their original release, and we therefore know that they were alive and could have been recovered at the most s times during the intervening period. Similarly, a number N_s of the Z_t will have been

last recovered at the s^{th} sampling, and these could have been recovered at the most $s-1$ times; and so on. We then examine the frequency distribution of recovery marks in each of these various groups of birds.

Suppose a particular group of N_{s+1} birds is known to have been alive over a period during which s samples have been taken from the general population. If n_i out of this group of N were recovered at the i^{th} sampling, then the probability that an individual member of the group bears the recovery mark i is given by

$$p_i = n_i/N \quad , (i = 1,2,3,\ldots,s).$$

Then putting $q_i = 1-p_i$,

we can calculate the probability that an individual will have been recovered 0, 1, 2, ... $(s-1)$, s times, assuming that the sampling of the individuals had been entirely at random.

The expected frequency distribution can be calculated by expanding

$$(p_1+q_1)\,(p_2+q_2)\,(p_3+q_3)\ldots\ldots\ldots\ldots(p_s+q_s),$$

and collecting the appropriate terms. This is the binomial distribution of Poisson (see *e.g.* Aitken 1939, § 23) for which the mean is

$$\mu = \Sigma p_i \quad ,$$

and the theoretical variance

$$\sigma^2 = \Sigma p_i q_i \quad .$$

It will be noted that if

$$p_1 = p_2 = p_3 = p_4 = \ldots. = p_s = p, \text{ say,}$$

then the expected distribution would be given by the expansion of the ordinary Bernoullian binomial $(p+q)^s$, for which the mean and variance are

$$\mu = s\,p\ ,$$
$$\sigma^2 = s\,p\,q\ .$$

If the differences between the p_i are small, the use of the ordinary binomial would be a satisfactory approximation to the expected distribution.

It would, of course, be possible to calculate the expected numbers of recoveries by means of either of these two theoretical distributions, and to compare the expected and observed frequencies by means of a goodness of fit test. But this procedure would be lengthy, particularly if we had to deal with a large body of data. A more simple, and at the same time a more sensitive, test is to compare the observed and expected variances of the distribution (Cochran 1954).

Given the observed frequency distribution of recoveries among the N birds, we first of all calculate in the usual way the sum of the squares of the deviations from the mean, $\Sigma(x-x^2)$; and then the ratio

$$X^2 = \frac{\Sigma(x-x)^2}{\sigma^2}$$

where the expected variance,

$$\sigma^2 = \Sigma p_i q_i \quad .$$

Then, provided that s and N are not too small, we can assume that X^2 is distributed approximately as a χ^2 with $N-1$ degrees of freedom. It is difficult to lay down hard and fast rules; but it may be suggested that for this approximation to hold, s should not be less than 3, and that N should be greater than 20 individuals.

Numerical example

In 1946, 1440 adult shearwaters were ringed for the first time, and out of these a group of 32 individuals were last recovered in 1952. The number recaptured (n_i) in each of the five years between 1946 and 1952, together with the observed frequency distribution of x, the number of times each individual was recaptured, were as follows:

Year	n_i	x	$f(x)$
1947	7	0	15
1948	7	1	7
1949	6	2	7
1950	4	3	2
1951	7	4	1
		5	0
		Total	32

Then, $\mu = \Sigma n_i/N = 31/32 = 0{\cdot}9688$, which is the same as the mean of the frequency distribution, $\bar{x} = \Sigma x f(x)/N = 0{\cdot}9688$. We then have

$$\Sigma(x-\bar{x})^2 = \Sigma x^2 f(x) - [\Sigma x f(x)]^2/N$$
$$= 69 - 30{\cdot}03 = 38{\cdot}97.$$

For the theoretical variance, we have

$$\sigma^2 = \Sigma p_i q_i = \mu - \Sigma n_i^2/N^2 = 0{\cdot}9688 - 0{\cdot}1943 = 0{\cdot}7745.$$

Hence $X^2 = 38{\cdot}97/0{\cdot}7745 = 50{\cdot}32.$

Treating this as a χ^2 with 31 degrees of freedom, and using the usual approximation that for a number of degrees of freedom as large as this, $\sqrt{2\chi^2} - \sqrt{2d.f.} - 1$ is distributed normally about zero with unit standard deviation, we have

$$\sqrt{100{\cdot}6} = 10{\cdot}03$$
$$\sqrt{61} = 7{\cdot}81$$
$$\text{Difference} = +2{\cdot}22$$

Thus, the probability of obtaining a value of χ^2 as great or greater than this is somewhere between $P = 0{\cdot}025$ and $P = 0{\cdot}01$. We conclude, therefore, that the variability in the frequency of recapture of these 32 individuals was significantly greater than that expected if they were being sampled at random. The suggestion from the figures is that some birds were turning up in the samples more, and others less, frequently than expected. Thus, for example, from the n_i figures given above, we can calculate that the probability of an individual not being recaptured during the five years, assuming a random sampling of the population, was $q_1q_2q_3q_4q_5 = 0{\cdot}3390$, and therefore out of a total of 32 we should expect a frequency of 10·8 in the $x = 0$ class, whereas actually there were 15 birds observed.

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THE CLADOCERA AND COPEPODA (CRUSTACEA) OF THE TARNS OF THE ENGLISH LAKE DISTRICT

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(With 2 Figures in the Text)

Previous work on the tarns of this district has been limited both in extent and time. Beck (1883), Brady (1868), Gurney (1923) and Scourfield (unpublished data) give the names of only eighteen tarns and most of these were visited at only one season, July to September. When an algal and chemical survey of the tarns was started by this Association in 1953, the opportunity was therefore taken to make a comprehensive survey of the Cladocera and Copepoda as well. Between 1953 and 1956, 144 tarns were visited and their names are listed alphabetically in the appendix, together with national grid references, surface areas, heights above sea-level, depths and months of collecting.

The topography of the district is well known and fully described elsewhere, so here only the salient features are briefly described. The district has the general shape of a wheel 48 km in diameter, with a central hub of hard non-calcareous rock rising to eight summits over 900 m and about fifty over 600 m, from which spurs separated by glaciated valleys, in many of which are lakes, radiate out to a low-lying periphery of carboniferous limestone. The most satisfactory definition of the Lake District for the ecologist is probably that of Marr (1916) whose geological boundary separates reasonably clearly the hard lime-deficient rocks of the district from the encircling limestone area, except in the south where there are some irregular outcrops.

In the popular view, a tarn is a body of water intermediate in size between a lake and a pool. Macan (1950) found a useful distinction between tarns and lakes to be the common species of emergent plant which was *Phragmites communis* Frin. in lakes but *Carex rostrata* Stokes in tarns, and between tarns and pools to be the presence or absence of a perennial outflow, which is present in tarns but not in pools. According to these criteria, most of the waters visited in this survey are tarns but a few such as Loughrigg Tarn and Little Langdale Tarn are lakes. The surface area of 80% of the waters lies between 5000 and 50 000 m^2 and only four exceed 200 000 m^2.

As a preliminary step in grouping, the tarns were arranged according to altitude and total ionic concentration expressed in milli-equivalents per litre. Three more or less distinct groups are then apparent: (1) the high tarns, those over 275 m and low in total ions (< 0·8 m-equiv./l.), (2) the tarns of the spurs and valleys within Marr's geological boundary, those below 275 m and low in total ions (< 1·0 m-equiv./l.) and (3) the outlying tarns either outside or only just inside

Marr's boundary, those below 200 m and high in total ions (>1·0 m-equiv./l.). These three groups were next subdivided according to a visual appreciation of the amounts of aquatic weeds which they supported. Group 1 was divided into three groups: (1*a*) the relatively deep rocky tarns with barren shores, (1*b*) tarns with mostly rocky shores but some weed-beds, and (1*c*) shallow tarns with extensive weed-beds and much marginal sphagnum. Groups 2 and 3 were each divided into subgroups: (*a*) those with relatively large areas in the centre free of weeds and (*b*) those in which this area is small.

COLLECTING AND METHODS

Collecting was done with a black conical net, 60 meshes to 2·5 cm which was usually cast on a line from the shore, but in fifteen of the larger tarns the deep water was also sampled from a dinghy. Samples from different habitats, *e.g.* open water, rocky shore, weed-bed, were kept separate. No regular programme of collecting was possible but most tarns were visited at more than one season and one, Goatswater, was visited fortnightly throughout 1955.

Preliminary examination of samples was done in a counting trough using low-power magnifications of a binocular microscope. The whole of each sample was sorted in the trough, in successive fractions when necessary, and the abundance of each species noted as, abundant (>150), numerous (20-150) or scarce (<20). Identification of species, except those which could be recognized with certainty in the trough, was done under high power. Cladocera were named according to Scourfield & Harding (1941) and Copepoda from Gurney (1931-33).

RESULTS

(*a*) *General*

Fifty-three species of Cladocera and twenty-eight of Copepoda were found. Thirty-nine species were distributed among fewer than ten tarns and only two species, the cladoceran, *Chydorus sphaericus* and the copepod *Cyclops agilis* were found in more than ninety tarns. All species were found in tarns which were geographically widely scattered. The distribution of many species is correlated more closely with the presence of aquatic weeds or the character of the bottom than with altitude or chemistry of the water. Although only rough estimates of population numbers were possible, it was noted visually that in those tarns with extensive weed-beds the open water and the weed-beds appeared to have equally abundant populations, whereas in tarns with virtually no weed-beds population numbers in-shore were usually low, but in the deep water unexpectedly large and in marked contrast to the impression of barrenness gained from shore collecting. In weed-beds there were usually larger populations among thick-growing, many-branched plants like *Nitella* and *Myriophyllum* than among the straight emergent stems of plants such as *Carex* and *Equisetum*.

(b) Distribution of species according to tarns

The mean number of species (range 9-15) was similar in each group of tarns, probably because not even the rocky tarns of group 1*a* are wholly barren and also because several species are ubiquitous. Figs. 1 and 2 show the distribution of

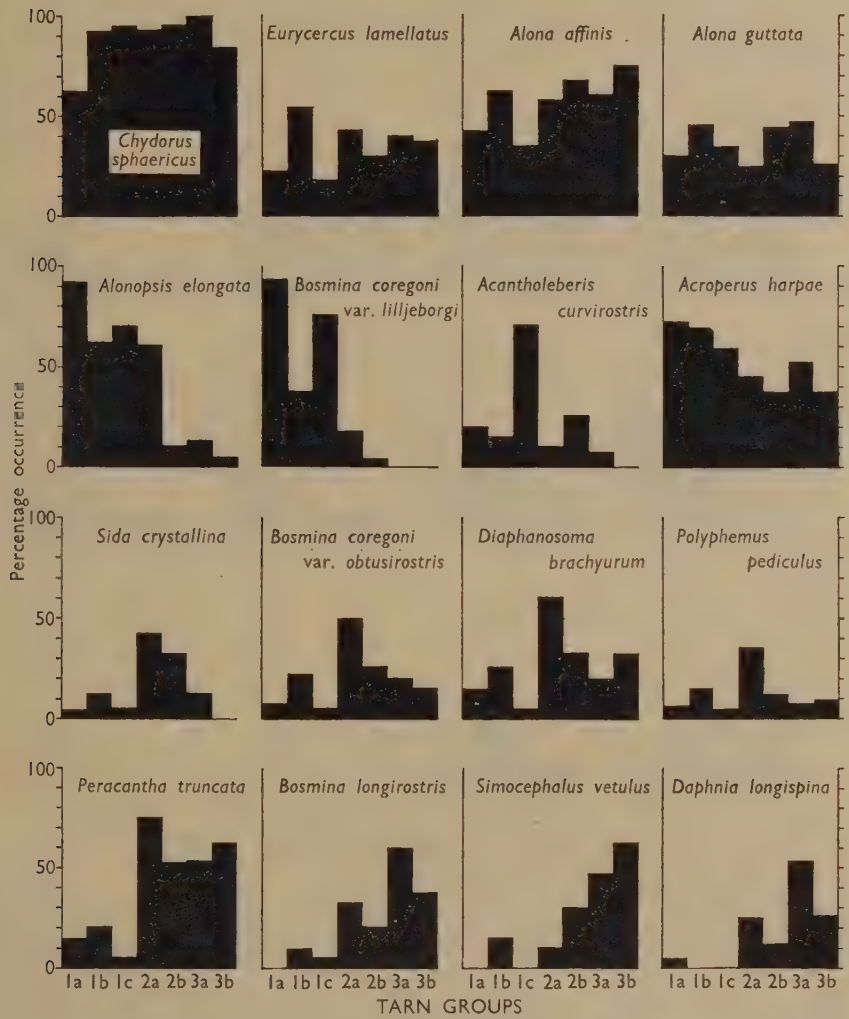

Fig. 1. The distribution of sixteen species of Cladocera in seven groups of tarns. The histograms show the percentage of the tarns in each group which contain the species.

Group 1 comprises the tarns of the high fells divided into: 1*a*, 26 deep, rocky tarns with few weeds; 1*b*, 13 rocky tarns with some weed; 1*c*, 17 shallow tarns with much *Sphagnum*.

Group 2 includes the tarns of the ridges and valleys divided into: 2*a*, 28 tarns with a large proportion of open water; 2*b*, 27 tarns with little open water.

Group 3, the outlying tarns, is similarly divided into: 3*a*, 15 tarns with much open water, and 3*b*, 19 tarns with little.

sixteen species of Cladocera and ten species of Copepoda which were found in twenty or more tarns. It can be seen that *Chydorus sphaericus*, *Eurycercus lamellatus*, *Alona affinis*, *A. guttata*, *Diaptomus gracilis*, *Cyclops agilis* and *C. viridis* are ubiquitous. Other species are restricted in range and can be grouped as follows: (*a*) *Alonopsis elongata*, *Bosmina coregoni* var. *lilljeborgi* and *Acroperus harpae* are most frequently found in the high rocky tarns; (*b*) *Bosmina coregoni* var. *obtusirostris*, *Diaphanosoma brachyurum*, *Sida crystallina* and *Polyphemus pediculus*

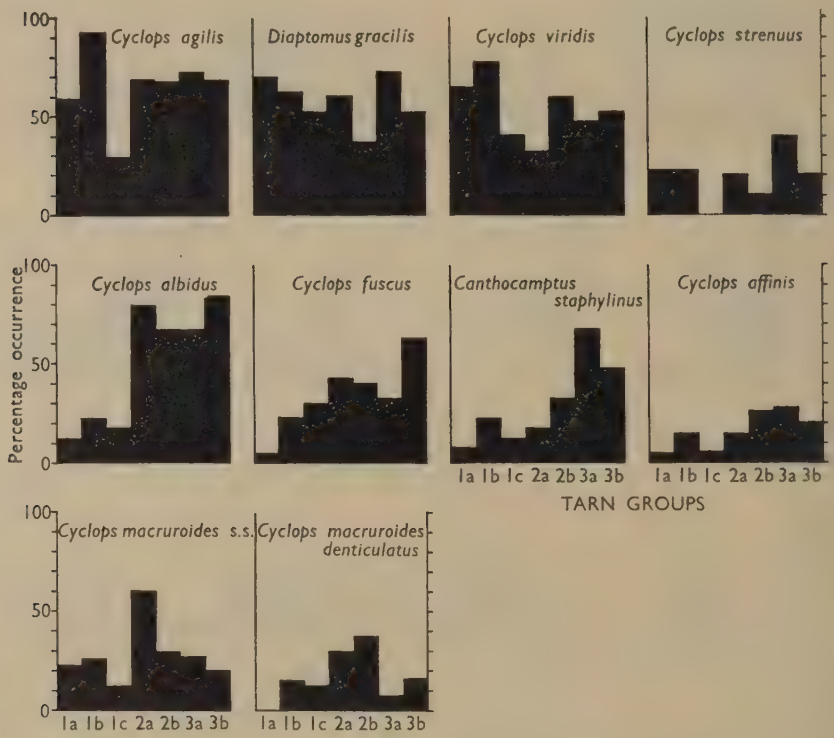

Fig. 2. The distribution of ten species of Copepoda in the same seven groups of tarns as Fig. 1.

are most frequent in the intermediate tarns of group (2); (*c*) *Peracantha truncata* and *Cyclops albidus* are rare in the high tarns but equally common in the other groups; and (*d*) *Cyclops fuscus*, *Canthocamptus staphylinus*, *Cyclops affinis*, *Bosmina longirostris* and, in particular, *Simocephalus vetulus* and *Daphnia longispina* are most frequently found in the low-lying weedy tarns of group 3.

(*c*) *Distribution of species according to habitats*

The crude sampling technique permits only a broad outline of ecological relationships for most species. Table 1 shows that the largest numbers of species

are to be found in weed-beds, moderate numbers in open water, and only a few on barren shores. Certain species are characteristic of particular habitats, *e.g.* *Alonopsis elongata* on rocky shores, *Acantholeberis curvirostris* among sphagnum, *Diaptomus gracilis*, *Bosmina* spp., *Cyclops strenuus* and *Daphnia longispina* in open water.

Table 1. *The percentage occurrence of the more common species in four habitats*

	Open water	Shore		
		Rocky	Weedy	Sphagnum
Number of samples	87	40	89	30
Diaptomus gracilis Sars	69	22	27	10
Bosmina coregoni var. *lilljeborgi* (Sars)	43	25	6	0
Cyclops strenuus Fischer	23	6	6	0
Diaphanosoma brachyurum (Liéven)	22	3	11	0
Daphnia longispina (O.F.M.)	21	0	1	0
Ceriodaphnia pulchella Sars	17	0	15	0
Bosmina longirostris (O.F.M.)	14	0	9	0
B. coregoni var. *obtusirostris* (Sars)	10	0	6	0
Chydorus sphaericus (O.F.M.)	15	6	60	50
Cyclops agilis Koch	0	8	43	0
Peracantha truncata (O.F.M.)	0	0	31	10
Cyclops albidus Jurine	0	0	27	0
Eurycercus lamellatus (O.F.M.)	0	0	22	0
Sida crystallina (O.F.M.)	0	0	21	0
Polyphemus pediculus (L.)	8	3	16	0
Cyclops viridis (Jurine)	0	3	13	0
Alonopsis elongata Sars	0	89	13	0
Simocephalus vetulus (O.F.M.)	0	0	12	0
Cyclops fuscus Jurine	0	0	10	0
C. macruroides s.s. Lilljeborg	0	0	10	0
Alona affinis (Leydig)	0	6	9	15
Acroperus harpae Baird	1	14	8	10
Canthocamptus staphylinus (Jurine)	0	0	7	0
Alonella excisa (Fischer)	0	0	7	10
Acantholeberis curvirostris (O.F.M.)	0	0	3	100
Number of species in more than 5% of the samples	10	8	23	7

(*d*) *Comparison with earlier collections*

It may be an indication of the effective means of dispersal possessed by most Entomostraca that very little difference is apparent between the list of common species collected in the present survey and that of the earlier collectors in spite of the small number of tarns visited by them. From the earlier records, I have made out a list of thirty-five species of Cladocera and twenty-one of Copepoda from eighteen tarns of which all but six cladocerans and five copepods (all uncommon species) were found again in these particular tarns, and eight of these eleven missing species were found in other tarns in the district. My list for the 144 tarns visited in the present survey includes nineteen additional species of Cladocera and ten of Copepoda but most are scarce species found in the outlying tarns and only

three, two cladocerans *Simocephalus vetulus* and *Pleuroxus trigonellus* and one copepod, *Cyclops macruroides* s.s. are common.

The records for each tarn separately present a greater contrast, for only fifty-two out of 138 records for Cladocera are confirmed and seventy-seven new ones added, and forty out of fifty-two for Copepoda with thirty-two new ones added. These differences in the records for each tarn separately are for several reasons not unexpected. Many of them are for species which were not very numerous and the chances of catching or missing such species are probably about equal. Moreover, it is well known that Crustacea vary greatly in their seasonal abundance and most earlier collecting was done in only July, August and September. Furthermore over half of the unconfirmed records are from three tarns Loughrigg, Lily Tarn (Loughrigg) and Clay Pond (Wray Castle) which Scourfield visited eight or nine times compared with only one or two visits to other tarns and virtually all my new records are from tarns which Scourfield did not go to. In these latter tarns, population changes since the time of Brady and Gurney cannot be ruled out, but it seems more likely that my new records result from collecting at more than one season. It is remarkable that Gurney has no record of the ubiquitous *Chydorus sphaericus* and Brady only one.

(*e*) *Distribution and ecology of species*

(The number of tarns in which each species was found is given in parentheses after the specific name.)

Suborder CLADOCERA

Family Sididae

Sida crystallina (O. F. Müller) (29). Among weeds; in particular under or attached to floating leaves of *Potamogeton* spp. and only occasionally in *Carex* beds and thick weed-beds. Present most frequently in tarns under 275 m and with less than 1·0 m-equiv./l. The absence of this species from all but two of the thirty-four tarns under 200 m and with more than 1·0 m-equiv. l. is difficult to account for, as many of these appear to be similar in amount and kind of weeds to those in which the species has been found.

Diaphanosoma brachyurum (Liéven) (46). More common in the open water than among weeds and more frequent in tarns under 275 m and with less than 1·0 m-equiv./l. than in other groups of tarns.

Family Holopedidae

Holopedium gibberum Zaddach (4). Only abundant in open water. In Blea Water (Haweswater), Easedale and Seathwaite Reservoir and probably also in Overwater, where the open water was not sampled but a single specimen was caught in shore collecting. These tarns are among the largest and deepest in the district, as well as being over 200 m in altitude and low in total ions.

Family Daphniidae

Daphnia hyalina s.s. Leydig (13). Only in open water. Most of the tarns in which it occurred are among the largest in the district but there is no relation between these tarns and either altitude or ionic concentration.

Daphnia longispina (O. F. Müller) (24). Only in open water. More frequently found in tarns under 275 m and over 1·0 m-equiv./l. than in high tarns of lower ionic concentration. In previous records for this district, this species has almost certainly been described as *D. hyalina* to which it is closely related taxonomically but as Johnson (1952) has pointed out, there are reasons for regarding it as a separate species.

Daphnia obtusa Kurz (4). Found in Tarn, Berrierend, Skelsmergh and Black Moss, all less than 10·0 m² in area, with much weed, and only 1-2 m deep and situated on the fringes of the district.

Daphnia pulex (De Geer) (1). Found only in Decoy Pond near Penrith, a small shallow pool full of water weeds, situated on the north-eastern fringe outside Marr's geological boundary. This record seems to be the most northerly for the species.

Scapholeberis mucronata (O. F. Müller) (8). All the ponds in which this species was found are in sheltered positions. Not found above 275 m.

Simocephalus vetulus (O. F. Müller) (32). Among weeds. Found mostly in low-lying tarns high in total ions.

Simocephalus exspinosus (Koch) (8). Among weeds. In Bigland, Lambrigg, Yew-tree, Sprinkling, Scale, Hodson, Wise Een and Clay Pond.

Ceriodaphnia reticulata (Jurine) (9). Among weeds. In tarns differing widely in size, altitude and total ions but all with weed-beds.

Ceriodaphnia megalops Sars (4). In thick Carex. The four tarns are less than 15·0 m² in area, shallow and rich in weeds.

Ceriodaphnia quadrangula (O. F. Müller) (14). Mostly in open water but occasionally abundant in weeds. Found in tarns of all kinds.

Ceriodaphnia pulchella Sars (35). Common in open water and also among weeds. Rarely found in tarns over 275 m but at lower levels it occurs in tarns of all kinds.

Ceriodaphnia affinis Lilljeborg (2). Found only in Whins and Mere, both lying just outside Marr's geological boundary.

Family Bosminidae

Bosmina longirostris (O. F. Müller) (35). Mostly in open water but occasionally abundant in weeds also. Most frequently found in low-lying tarns high in total ions.

Bosmina longirostris s.s. was present in most tarns but var. *similis*, var. *brevicornis* and var. *cornuta* were also found in a few tarns, sometimes together with *B. longirostris* s.s.

Bosmina coregoni var. *obtusirostris* (Sars) (Syn. *B. obtusirostris* Sars. Scourfield & Harding 1941) (33). Abundant in open water, but occasionally among weeds. Present in a wide variety of tarns but most frequently found in those tarns under 275 m and under 1·0 m-equiv./l.

Bosmina coregoni var. *lilljeborgi* (Sars) (Syn. *B. lilljeborgi*, Sars. Scourfield & Harding 1941, *B. mixta* Lilljeborg) (48). Most frequently found in open water. A species characteristic of high tarns, those over 200 m and low in total ions and found as frequently in deep rocky tarns as in shallow peaty tarns. This variety is distinguished from *B. coregoni* var. *obtusirostris* by the relative lengths of shell spine and the claw with the process bearing it, the shell spine in var. *lilljeborgi* being much shorter than the claw and the process bearing it whereas in var. *obtusirostris* these characters are similar in length. Only adults of the var. *lilljeborgi* have relatively short shell spines; the young in the brood pouch can be seen to have long shell spines similar to var. *obtusirostris*. In most instances, in casual observation, I find little difficulty in assigning most specimens in a population to either one variety or the other, but in a few tarns both varieties were present together. Although Scourfield & Harding (1941) do not record this form from the Lake District, the reason is probably taxonomic, for although it is puzzling that Scourfield who collected in five tarns over 275 m. Easedale, Codale, Angle (Bowfell), Grisedale and Red (Helvellyn), does not record it, I have little doubt that the short-spined Bosminas which Gurney (1923) found in Floutern Tarn and Goatswater are the same as mine.

Family Macrothricidae

The members of this family live mainly on the bottom either in mud or decaying organic matter and probably for this reason are often recorded as rare.

Ilyocryptus sordidus (Liéven) (23). In mud on the bottom. Adults always have some mud adhering to the back and sides but young often have no attached mud. Present in a wide variety of tarns.

Ilyocryptus acutifrons Sars (1). Two specimens from Overwater, a large tarn on the northern outskirts of the district.

Streblocerus serricaudatus (Fischer) (15). Among weeds, especially in *Sphagnum* and the swampy margins of shallow tarns. Present in tarns differing widely in total ions and in altitude.

Drepanothrix dentata (Eurén) (20). Abundant in decaying vegetation on the bottom. Present in tarns differing widely in total ions and in altitude.

Acantholeberis curvirostris (O. F. Müller) (30). Particularly common near *Sphagnum*. Virtually confined to shallow tarns, 1-2 m deep, with less than 0·6

m-equiv./l. in the water and mostly over 200 m in altitude. Ephippia were found in only July, August and September, although collecting was done throughout the year.

Family Chydoridae

Eurycercus lamellatus (O. F. Müller) (49). Among weeds on or near the bottom. Present in all groups of tarns.

Camptocercus rectirostris Schödler (6). Among weeds. A few specimens from three tarns in group 1*b* and three in 2*a*.

Acroperus harpae Baird (76). Usually among weeds but occasionally found in abundance in stony shores, *e.g.* Kentmere Reservoir where there are virtually no weed-beds. Present over the whole range of tarns.

Acroperus angustatus Sars (2). Among weeds. A few specimens from Lilymere and Ratherheath both outside Marr's boundary.

Alonopsis elongata Sars (67). On rocky exposed shores. The characteristic species of the margins of tarns over 200 m and low in total ions.

Alona affinis (Leydig) (83). On sandy bottoms and fine gravel near the margins of tarns, often among weeds but common on exposed shores also. An ubiquitous species present over the whole range of tarns and only exceeded in frequency of occurrence by *Chydorus sphaericus* (O. F. Müller).

Alona costata Sars (2). Among weeds. A few specimens from Middlerigg and Cunswick.

Alona guttata Sars (51). Mostly on muddy bottoms but occasionally among submerged moss. Found over the whole range of tarns.

Alona quadrangularis (O. F. Müller) (1). Only a few specimens on a stony shore in Kentmere Reservoir.

Alona rectangula Sars (20). In marginal weeds on the bottom. Not so frequently found as *A. guttata* but present over the whole range of tarns.

Alona rustica T. Scott (1). A single specimen from Bigland Tarn.

Rhynchotalona rostrata (Koch) (1). 2 specimens from Urswick Tarn (altitude 38 m, and 4·55 m-equiv./l.) which lies to the south outside the Lake District as defined by Marr's geological boundary.

Leydigia leydigi (Schödler) (1). A few specimens from Berrierend Tarn on the northern margin of the district. From mud on the bottom.

Graptoleberis testudinaria (Fischer) (36). On muddy bottoms, often but not always among weeds. Present in a wide variety of tarns.

Alonella excisa (Fischer) (28). On the bottom among weeds, but also on exposed rocky shores of tarns with virtually no weed-beds. Not found in tarns with more than 1·0 m-equiv./l.

Alonella exigua (Lilljeborg) (10). Among weeds, in particular floating leaves of *Potamogeton* and also on the bottom.

Alonella nana (Baird) (44). Among bottom debris and weeds. Present over the whole range of tarns.

Peracantha truncata (O. F. Müller) (64). Among weeds. More frequently found in low-lying tarns high in total ions than in the high hill tarns low in total ions.

Pleuroxus laevis Sars (6). Among mud and weeds. In tarns below 275 m except Greendale at 402 m.

Pleuroxus trigonellus (O. F. Müller) (11). Among mud and weeds. In tarns below 275 m.

Pleuroxus uncinatus Baird (1). Only found in Urswick Tarn where it was equally abundant with *P. trigonellus*. The outer surface of the shell is covered with fine particles of mud in all the specimens I examined, and by this feature alone I could separate the two species without error, as in *P. trigonellus* the shells are free of any adhering particles.

Pleuroxus aduncus (Jurine) (1). A single specimen from Whinfell Tarn which lies on the eastern margins of the Lake District.

Chydorus globosus Baird (9). Among weeds, and also on stony shores. Found in all groups of tarns.

Chydorus sphaericus (O. F. Müller) (127). Nearly always associated with weeds. Present in practically all the tarns in all groups except that of tarns over 275 m altitude, under 0·8 m-equiv./l., and with virtually no weed-beds; even in this group it was found in small numbers in more than half the tarns and in one, Kentmere Reservoir, it was numerous in a vertical haul in 10 m depth of water in the centre of the tarn and also abundant on the rocky shore. On Kirkfell, the lower tarn (620 m) which dries up in some years, had in the wet summer of 1954 no Entomostraca except an abundance of *C. sphaericus* although the upper pond (735 m) $\frac{1}{2}$ mile away had eleven other species, in addition to *C. sphaericus*, in both the wet summer of 1954 and the dry one of 1955.

Chydorus piger Sars (29). Among weeds and on the bottom. Equally common in all the groups of tarns lying within Marr's geological boundary, but only found in a single tarn, Mockerkin, outside this line.

Monospilus dispar Sars (2). One specimen from among weeds in Lingmoor, a shallow weedy tarn and five specimens from the rocky shore-line of Easedale, a deep rocky tarn with practically no weed-beds.

Anchistropus emarginatus Sars (1). A few specimens from Blea Tarn (Langdale) in August 1955.

Family Polyphemidae

Polyphemus pediculus (Linneus) (29). Both among weeds and in open water. Found in all kinds of tarns from shallow weedy ones to deep rocky ones but rather more frequent in tarns intermediate between these extremes.

Family Leptodoridae

Bythotrephes longimanus Leydig (2). In open water. Found in only two of the larger waters, Kendal Park Head Reservoir (two specimens in a shore throw) and Devoke Water where it was numerous in vertical hauls from a dinghy in the centre and in small numbers in samples with a net thrown by line from the shore.

Leptodora kindti (Focke) (3). In open water. Found in three of the larger waters, Stickle Tarn (Langdale), Grisedale (Helvellyn) and Devoke Water. Numerous in vertical hauls from a dinghy in the centre but only occasional specimens in a net thrown on a line from the shore. Scourfield recorded a single specimen from Easedale Tarn in July 1898.

Order COPEPODA

Family Diaptomidae

Diaptomus gracilis Sars (79). Mainly planktonic but often abundant in-shore both on open shores and among weeds. Equally common in all groups of tarns.

Diaptomus laticeps Sars (1). Planktonic. Found only in Goatswater. It is known from only two other waters in the Lake District, Haweswater (Gurney 1923) and Windermere (Wailes 1939). Thus this survey shows that this arctic and alpine species is not common in the high tarns of the district, as Gurney (1923) thought it might be. As little is known of the reproductive cycle, my data from fortnightly collections in Goatswater in 1955, mostly from the shore, are given here. From January to April the species was not caught; in May only nauplii were found; copepodids appeared early in June and were common by early July. Adult females with spermatophores were first taken on 22 July in shore collecting, and on the same date in collections from a dinghy in open water in the centre of the tarn there was an abundant breeding population in which adult females carried on average seventeen eggs per sac, a figure which may be compared with 8-9 eggs per sac normally found in Windermere. Moreover, at the same time vertical and horizontal surface hauls showed that adult males were more abundant deeper in the water than adult females. Copepodids form 70-80% of the population in September and October, and some adults and copepodids were taken in November and December. It is likely, therefore, that in this tarn there are two generations in the year.

Diaptomus castor (Jurine) (3). Found only in Lily Tarn (Loughrigg), Low Seathwaite and Legburthwaite. Pools that dry up in summer have been excluded from this survey, so this species, which is characteristic of such pools, may have a wider distribution than these few records suggest. Although shallow, Lily Tarn has never been known to dry up, and Legburthwaite only does so in exceptionally dry weather. In spring breeding populations were found, but in summer free swimming stages were rare and usually only egg-sacs of the species were found among detritus on the bottom. These egg-sacs (of which twenty-five

were found in Lily Tarn) were identical in appearance and in size and number of eggs with those carried by breeding females caught in the spring.

Family Cyclopidae

Cyclops fuscus Jurine (51). Among weeds. In laboratory cultures it is often seen hanging by the antennules from the surface film of water. Most frequently found in low-lying tarns rich in total ions but present in a wide variety of tarns. Apparently tolerant of low oxygen concentrations since, apart from *C. agilis* Koch, it was the only species in Legburthwaite when this tarn almost dried up in the exceptionally dry summer of 1955.

Cyclops albidus Jurine (78). Among weeds. Found over the whole range of tarns but most frequently in those at low altitudes and high in total ions.

Cyclops prasinus Fischer (12). Abundant near *Sphagnum*; often found with *Acantholeberis curvirostris*. Found in shallow mossy tarns or, if large, on stretches of shallow mossy shore.

Cyclops agilis s.s. Koch (93). Among weeds. Found in tarns of all kinds. The most ubiquitous copepod and only exceeded in frequency of occurrence by the cladoceran, *Chydorus sphaericus* (O. F. Müller).

Cyclops agilis speratus Lilljeborg (7). Among weeds. Always associated with *C. agilis* s.s. Varieties intermediate between this form and *C. agilis* s.s. are said to be common, but only one such form was found in this survey in Blea Tarn (Armboth).

Cyclops macruroides s.s. Lilljeborg (47). Among weeds. Found in all groups of tarns and frequently associated with the closely related *C. agilis* s.s.

Cyclops macruroides denticulatus Graeter (27). Among weeds. Although there seem to be few records of this variety in Britain it is quite common in tarns in this district, most of them small shallow tarns. I have found it in the same tarn with *C. agilis* s.s. nineteen times, with *C. macruroides* s.s. in only four tarns, and unaccompanied by either of these species in only four tarns and in only one of these latter tarns, Allcock, was it abundant.

Cyclops macrurus Sars (3). Among weeds. Found in Skeggles Water, Boretree and Loughrigg.

Cyclops fimbriatus Fischer (19). Among weeds and detritus. In a wide variety of tarns but rather infrequently found and always in small numbers.

Cyclops affinis Sars (23). Among weeds and detritus. In a wide variety of tarns but rather infrequently found and always in small numbers.

Cyclops phaleratus Sars (6). Among weeds. Found in small, shallow tarns at low altitudes, high in total ions and with an abundance of weeds.

Cyclops strenuus Fischer (28). In open water. I find it in tarns of all kinds, except those over 275 m which are shallow and have much *Sphagnum*. Practically all the specimens I have examined belong to the variety *abyssorum* but the species

is notoriously variable, and in some populations especially those in low-lying peripheral tarns, I have found individuals of *C. strenuus strenuus*.

Cyclops viridis (Jurine) (74). Mainly in weed-beds and in all kinds of tarns.

Cyclops vernalis Fischer (3). Found in Harrop, Tenter Howe and Tarn, all of them small shallow tarns with an abundance of vegetation.

Cyclops bicuspidatus Claus (4). Two of the tarns are small weedy ponds, which Gurney (1933) describes as the characteristic habitat of this species but the other two, Watendlath and Whins, are relatively large tarns.

Cyclops languidus Sars (1). A single specimen from Eel Tarn.

Cyclops nanus Sars (5). Among weeds in small shallow tarns all over 200 m with less than 0·35 m-equiv./l. and inside Marr's geological boundary.

Cyclops varicans Sars (2). A few specimens from among weeds in Parkgate and Chapel Hill.

Cyclops leuckarti Claus (8). In open water. Not above 275 m.

Cyclops dybowskii Lande (14). Among weeds. Apart from Sprinkling Tarn at 597 m altitude, the fourteen tarns in which I have found it are all between 100 and 200 m medium in size and with well-developed weed-beds. Although Gurney (1933) describes this species as rare in Britain it is more frequent in this survey than *C. leuckarti*, which it superficially resembles but from which it can be easily distinguished by the inner seta on the basis of leg 1; in *C. leuckarti*, the basis of leg 1 has no seta.

Family Harpacticidae

Although some harpactids, *e.g. Canthocamptus staphylinus* can be caught among weeds in the same way as *Cyclopoida*, many have specialized habitats, so that my records for this group are probably very incomplete.

Canthocamptus staphylinus (Jurine) (43). Among detritus on the bottom. Found in tarns of all kinds but more frequently in low-lying tarns high in total ions than in tarns on the high fells.

Canthocamptus pygmaeus Sars (8). From marginal weeds. Found in rather small shallow tarns but at all altitudes and over the whole range of ionic concentrations.

Canthocamptus zschokkei Schmeil (11). Among moss and on exposed shores under stones. Nine of the eleven tarns in which I find it are over 400 m in altitude and all have less than 0·5 m-equiv./l.

Canthocamptus crassus Sars (4). Among detritus on the bottom. Found in Browncove, Tewet and Whins, each different in character from the other two.

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SUMMARY

1. The distribution and ecology of Cladocera and Copepoda in 144 Lake District tarns was studied in a survey made between 1953 and 1956.

2. Although some species appear to be ubiquitous, there is a strong association between the distribution of many species and the presence or absence of aquatic weeds.

3. Fifty-three species of Cladocera and twenty-eight species of Copepoda were found, all of them in tarns widely scattered geographically. Only a few species were found in a high proportion of the tarns, and nearly half were distributed among ten or fewer tarns.

4. Although only sixteen tarns are known to have been visited in earlier collecting, only a few additional species have now been found, mostly rather scarce species and from tarns lying on the fringes of the Lake District.

5. Notes on the ecology of individual species, arranged taxonomically, are given.

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APPENDIX

List of the tarns visited

Depth determinations marked with an asterisk are taken from surveys made by the Brathay Hall Exploration Groups.

Tarn	National grid reference	Total ions (m-equiv./l.)	Altitude (m)	Surface area (ares = 100m²)	Depth (m)	Months of collecting
Allcock	35/349079	0·60	358	7	2	V, VI
Angle (Hartsop)	35/417144	0·53	480	58	9*	VII, XII
Angle (Bowfell)	35/244076	0·20	579	34	16*	VII, IX
Arlecdon	35/096196	0·40	229	163	4	IV, VI
Barfield	34/107869	0·65	24	32	–	VII

Tarn	National grid reference	Total ions (m-equiv./l.)	Altitude (m)	Surface area (ares = 100m²)	Depth (m)	Months of collecting
Barrow Res 1	34/256789	1·25	122	110	–	VII, VIII
Barrow Res. 2	34/244785	1·25	153	90	–	VIII
Barrow Res. Tarn	34/258782	1·44	122	10	–	VIII
Beacon	34/273901	0·74	163	46	–	VI, VII
Berrierend	35/421294	0·51	281	12	5	VII, VIII
Bigland	34/355829	1·11	168	53	–	IX
Black Moss	34/548972	1·23	160	8	–	IV, V, IX
Blackbeck	35/201128	0·19	472	9	–	III, VII, VIII
Blea (Armboth)	35/292141	0·25	476	86	14*	VIII, X
Blea (Eskdale)	35/165010	0·41	213	33	–	I, VIII, IX
Blea (Langdale)	35/293044	0·27	187	37	–	VIII, IX
Blea Water	35/449108	0·31	483	174	68*	IV, VIII, X
Bleaberry	35/167155	0·29	503	11	6*	V, VII
Blind	34/263967	0·39	572	5	6	IV, VI, VIII, X
Boretree	34/355874	0·61	206	43	–	VI, X
Bowscale	35/336313	0·27	480	28	17*	VIII, X
Brathay Quarry	35/358018	2·40	95	5	3	X
Brigham	35/083308	2·42	53	27	–	VII
Brown Cove	35/343160	0·34	625	7	–	VII, IX
Burnmoor	35/184044	0·28	254	240	–	VIII, XII
Caldwell	35/357018	1·06	95	5	3	X
Chapel Hill	34/106978	0·96	152	12	–	V, VII
Clay Pond	35/373009	1·10	48	0	2	IX, X
Cleabarrow	34/424963	1·25	170	5	–	IV, IX
Codale	35/297088	0·22	466	14	7*	VII, VIII, IX, XII
Crook Res.	34/445957	0·98	200	7	–	VII
Cunswick	34/490938	3·91	145	84	–	VI
Dalehead	35/230153	0·23	503	3	–	VIII
Decoy	35/532226	0·64	270	8	2	IV, VII
Devoke Water	34/158969	0·48	233	280	–	VIII
Dock	35/274144	0·39	403	19	5*	VI
Easedale	35/308087	0·21	279	106	21*	VII, VIII, IX, XII
Eel	35/189019	0·29	198	15	–	VIII, IX, XII
Floutern	35/124170	0·29	381	15	4*	V, IX, X
Garnett Bridge	34/515991	0·56	260	7	–	IV, VI
Ghyll Head	34/398923	0·70	119	31	–	IV, VII
Goatswater	34/266977	0·37	502	25	13	All
Grayrigg	34/596981	0·80	221	19	–	VII
Greenburn	35/284021	0·25	297	10	–	IX
Greendale	35/148074	0·33	402	20	9*	III, V, VIII
Grey Knotts	35/218125	0·22	625	8	1	V
Grice Croft	34/171858	0·56	77	40	–	VII
Grisedale	35/349120	0·29	539	120	35*	VI, VII, IX
Grizedale	34/346944	0·47	240	4		IV
Gurnal Dubs	34/502992	0·53	290	32	–	IV, VI
Hard	35/346138	–	716	5	–	VII
Harrop	35/312137	0·26	290	15	–	VII, IX, X
Hayeswater	35/432122	0·50	422	167	17	IV, VII
Hazel Mount	34/189869	1·28	77	4	–	VII
High Arnside	35/332012	0·56	168	8	–	VII
High Beauthwaite	34/253843	0·91	242	2	–	IV
High Borran	35/429010	0·83	200	36	–	VII
High Dam	34/362888	0·60	175	52	–	VIII, X
High House	35/241094	0·16	655	1	2	VII
High Nook	35/124199	0·29	221	7	2	V, VII
High Scawdel	35/232147	0·14	549	0	1	VIII
Hodson	34/369982	0·49	221	4	3	All
Holehird	35/409009	1·16	110	9	–	VII
Holme Ground	35/315011	0·27	230	5	3	VIII
Hood	34/571875	1·23	123	5	–	VI, XII

Tarn	National grid reference	Total ions (m-equiv./l.)	Altitude (m)	Surface area (ares = 100m²)	Depth (m)	Months of collecting
Innominate	35/198129	0·18	533	5	1	III, VII, VIII
Kemp	34/465988	1·25	250	1	1	VII
Kendal, Park Hd. Res.	34/552930	0·85	225	139	–	VII
Kendal, Sleddale H. 1	34/535935	0·83	116	15	–	V
Kendal, Sleddale H. 2	34/537935	1·09	116	9	–	V
Kentmere	35/444080	0·43	290	173	10	VI
Kirkfell (upper)	35/197107	0·18	740	0	1	VII, VIII
Kirkfell (lower)	35/207108	0·19	620	0	1	VII, VIII
Kitmere	34/603855	0·67	207	51	–	VII
Knipe	34/427944	0·88	145	21	4	V, VII
Knittleton (large)	34/255859	1·10	137	16	–	VIII
Knittleton (small)	34/256864	1·23	137	5	–	VIII
Knottalow	34/272803	1·26	206	23	–	VII
Lambrigg	34/583948	0·54	300	7	–	VII
Langhowe	35/318068	0·41	369	8	1	VIII
Latrigg	35/416018	0·82	245	2	–	IV, VII
Legburthwaite	35/314197	0·62	175	1	1	V, VI, VIII, IX
Levers Water	34/279993	0·26	411	152	38*	IV, VII, VIII
Lily (Loughrigg)	35/364040	0·34	200	1	1	IV, VII, VIII
Lilymere	35/604915	0·55	214	146	–	VII
Lingmoor	35/302051	0·33	396	4	2	IV
Little	35/249338	0·86	198	13	–	V
Little Langdale	35/308032	0·32	104	73	–	VIII, IX
Littlewater	35/509169	1·47	259	15	–	IV, VIII
Loughrigg	35/343044	0·66	94	86	–	IX
Low	35/163094	0·20	480	34	3*	VII
Low Water	34/275983	0·29	544	17	14*	IV, VIII, X
Low Scathwaite	34/291825	0·54	138	8	–	IV
Lowick Common	34/293849	0·70	107	2	–	IV
Mere	34/267718	5·28	30	17	–	VII
Middle Fairbank	34/450973	0·70	200	42	–	VII
Middlerigg	35/396011	0·92	84	11	–	V, VI
Mill Dam	34/461952	1·70	155	0	–	IV
Mockerkin	35/083232	1·08	115	35	3	IV, VI
Moss-side	34/484956	1·64	100	7	–	VIII, IX
Over Water	35/252350	0·81	198	220	–	V
Parkgate	35/118006	0·72	58	34	–	V
Rather Heath	34/484958	1·12	114	21	–	IV, IX
Red (Helvellyn)	35/349152	0·26	718	98	25*	VII, IX
Red (Langdale)	35/267037	0·19	503	7	1	VII, IX
Scale	34/374975	0·50	240	6	3	All
Scales	35/329282	0·22	610	10	8*	VIII, X
Scandale	35/385097	0·38	564	1	–	V, VII
School Knotts	34/428973	0·68	213	4	–	VII
Scoat	35/159104	0·19	602	52	20*	VII
Seathwaite	34/253988	0·30	366	267	26	IV, VI
Siney	35/162012	0·31	221	7	–	VIII, IX
Skeggles Water	35/479034	0·47	320	47	3	IV, V
Skelsmergh	34/534967	4·26	109	8	–	V
Small Water	35/454100	0·38	452	46	16*	IV, VIII
Sprinkling	35/228092	0·23	597	25	9*	VII, VIII
Stickle (Dunnerdale)	34/214928	0·81	300	3	2	V
Stickle (Langdale)	35/287076	0·23	469	91	16	IV, VII
Sticks	35/357181	–	575	30	–	VII
Stony	35/199024	0·24	297	12	–	VIII, XI
Styhead	35/222099	0·27	436	21	6*	VII, VIII
Sunbiggin	35/676077	2·79	251	46	–	IX
Tarns	35/116474	1·01	15	–	2	IV, VII
Tarn-at-leaves	35/258122	0·18	518	7	–	IX
Tarnhouse	34/577843	1·04	168	19	–	XII

Tarn	National grid reference	Total ions (m-equiv./l.)	Altitude (m)	Surface area (ares = 100m²)	Depth (m)	Months of collecting
Tarn Hows	35/331000	0·57	188	144	–	VIII
Tenter Howe	35/507007	0·34	251	5	–	V, VI
Terry Bank	34/592825	1·26	152	50	–	XII
Tewet	35/304237	0·53	198	15	–	V, VI
Tewit How	35/146118	·	602	5	1	VII
Torver	34/281926	0·71	114	29	–	VII
Tosh	35/128052	0·56	84	9		V
Urswick	34/270745	4·55	38	48	–	· VII
Watendlath	35/275162	0·29	258	40	17	VI, VIII, IX
Wharton	34/331988	0·78	198	12	–	V
Whinfell	34/559980	3·09	126	55	–	IV, V
Whins	35/555308	1·88	100	145	·	IV, VI
Whitemoss	35/346068	0·64	114	0	1	IV, VI
Windermere Res.	35/422018	0·77	222	34	·	IV
Wise Een	34/370975	0·50	229	44	3	All
Witherslack Hall	34/435864	3·29	61	26	–	IV
Woodhow	35/136043	0·54	61	12	–	V, VII
Yewtree	35/322004	0·42	107	38	–	VII

THE DISTRIBUTION OF SOME FRESH-WATER INVERTEBRATES IN PONDS IN RELATION TO ANNUAL FLUCTUATIONS IN THE CHEMICAL COMPOSITION OF THE WATER*

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(With 5 Figures in the Text)

Attempts have often been made to correlate the composition of the fauna of small bodies of standing water with certain chemical features of the environment. A number of interesting facts have come to light as a result of this approach. For instance, some fresh-water animals are known to be absent from ponds containing only small amounts of calcium, yet their occurrence has frequently been noted in large bodies of water of similar hardness. However, the data used in these studies have often been drawn from only one or a few visits to each locality. Since such factors as heavy rainfall have a marked effect upon the chemical constitution of the water, it seems unlikely that data of this kind give a true indication of the conditions that prevail throughout the year.

This paper contains an account of a survey of sixteen ponds, extending over a period of 14 months. Since calcium is recognized as one of the most important elements for organisms living in fresh water, it was decided to investigate its importance as a factor limiting the distribution of certain invertebrate animals in soft waters. The localities studied were therefore selected so as to include a range of calcium concentrations from approximately 5 to 45 p.p.m. In a preliminary investigation a large number of ponds was examined, and fifteen of these were selected for further study. In addition, a very hard-water lake was chosen for comparison.

During the period of investigation the seasonal fluctuations of a number of chemical constituents of the water were studied, and the distribution of certain invertebrate animals in the ponds was thoroughly examined. It was decided to collect molluscs, leeches and flatworms, as these animals represent the bulk of the larger members of the soft-bodied fauna inhabiting fresh water. In addition, *Asellus* and *Gammarus* were collected. It was considered that, unlike the aquatic insects, these animals would be particularly sensitive to the chemical composition of the water because their bodies are either directly exposed to the external medium, or enclosed in a casing composed largely of calcium salts.

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Table 1. *Physical characteristics of the sixteen ponds*

	Mean depth (ft)	Max. depth (ft)	Area depth ($ft^2 \times 10^3$)	Volume ($ft^3 \times 10^3$)	July inflow (ft^3/h)	National grid ref.	Surrounding vegetation	Rooted vegetation	Substratum	Surface weed (*Riccia*, *Lemna*)
Round Pond	0·39	1·39	15·3	5·96	Nil	41/966641	Pine, oak	*Juncus*, *Poa*	Deep layer of decaying leaves and other vegetation	Present
Chapel Row	0·71	1·41	4·7	3·45	Nil	41/581699	Oak, hazel	*Juncus*	Decaying leaves	Present
Farley	1·05	2·07	17·1	17·96	Nil	41/747647	Grazing pasture	*Sparganium*	Decaying vegetation	Present
Eagle	1·08	2·16	18·0	19·40	Nil	41/837624	Deciduous trees	*Juncus*, *Elodea*, *Typha*, *Nymphaea*	Decaying leaves	Present
Gormoor	1·41	2·82	63·9	90·10	55·1	41/871659	Pine, Rhododendron	*Sphagnum*, *Potamogeton*, *Nymphaea*	Finely divided peaty matter	Absent
Three Firs	1·77	3·57	17·1	30·27	Nil	41/653662	Heathland	*Potamogeton*	Finely divided peaty matter, stony areas	Absent
Egham	2·13	3·18	39·6	84·35	Nil	41/991698	Deciduous trees, some open ground	*Phragmites*, *Typha*, *Sparganium*	Decaying plant matter	Present
Hammond's	2·28	3·42	131·4	299·59	Nil	41/918624	Pine, Rhododendron	*Sphagnum*, *Potamogeton*	Finely divided peaty matter	Absent
Heath Lake	2·34	3·51	108·9	254·8	Nil	41/829653	Heathland	*Carex*, *Juncus*, *Phragmites*	Bagshot sand	Absent
Kiln Pond	2·37	3·57	383·4	908·7	1375·9	41/629633	Deciduous wood	*Juncus*, *Phragmites*	Decaying plant matter	Absent
Aldermaston	2·79	4·17	30·6	85·4	Nil	41/591638	Open ground	*Juncus*, *Phragmites*	Decaying plant matter, gravel	Absent
Leech	2·83	4·26	39·6	112·9	Nil	41/954644	Deciduous trees	*Typha*, *Phragmites*	Decaying plant matter	Present
Bagshot	3·03	6·12	207·8	639·5	768·7	41/931618	Oak, pine, alder	*Sparganium*, *Phragmites*	Gravel, some plant debris	Absent
Whiteknights	4·50	9·00	547·2	2462·4	54·0	41/737721	Deciduous trees, open ground	*Acorus*, *Sparganium*, *Phragmites*, *Typha*	Decaying plant matter	Absent
Heath Pond	4·83	6·42	90·9	439·1	Nil	41/812641	Pine	*Sphagnum*, *Typha*	Bagshot sand, peaty matter	Absent
Wasing	6·39	12·75	88·2	563·6	Nil	41/579633	Pine, oak	*Phragmites*, *Typha*	Decaying leaves, sand	Absent

METHODS

(*a*) *The physical characteristics of the localities*

Certain details relating to the physical characteristics of each pond appear in Table 1, where the localities are arranged in order of increasing mean depth. The mean depth of each pond was not determined precisely, but estimated after making a number of soundings. The amount of water flowing into open ponds (ponds receiving an inflow of stream water) was estimated by measuring the cross-sectional area and rate of flow of each inflowing stream.

(*b*) *The chemical factors studied and their estimation*

Total hardness and the calcium and magnesium contents were measured using the method described by Betz & Noll (1950). The total alkalinity was estimated by titrating a sample of the water with standard acid (0·02 N sulphuric acid), using xylene-cyanole-methyl-orange as indicator. The results were expressed as p.p.m. of calcium, so that comparison could be made with the values obtained by direct estimation of calcium. The colour (brownness) of the water was measured using a technique devised by Ohle (1934), and the results are expressed in Ohle units. The concentration of dissolved organic matter was estimated using the method described by Bennike (1943). The results are expressed in p.p.m. of potassium permanganate equivalent. A 'Doran' glass electrode pH-meter was used to measure the hydrogen ion concentration of both the water and the sub-aquatic soil. The sub-aquatic soil was placed in a 100 ml beaker to form a layer 1 cm deep, and about 50 ml distilled water were added. The whole was thoroughly mixed and allowed to stand for about 5 min. The pH of the supernatant liquid was recorded as the pH of the sub-aquatic soil.

Samples of water and of the sub-aquatic soil were taken from the littoral zone of each locality at monthly intervals. The water was collected in Kilner jars from areas of open water, and the samples of the substratum were taken from regions considered to be most representative of the whole locality. There was no evidence of variation from one part to another of a locality, but samples were always taken from the same areas throughout the period of regular sampling. Samples were analysed within 3 h of collection.

Many ponds froze during the first few months of investigation and samples from beneath the ice proved difficult to analyse, possibly because the stagnant water contained substances which interfered with the indicators.

During July 1956 samples were taken from Heath Pond, Hammond's, Leech and Egham, and the amount of free and albuminoid ammonia present in the water was estimated using the distillation method described by Thresh, Beale & Suckling (1949). The nesslerized distillate was measured colorimetrically using a Hilger 'Spekker' photometric colorimeter.

(*c*) *The fauna: methods of collection*

The following authorities were consulted for the identification of the species collected: Böhmig 1909 (flatworms), Chilton 1920 (*Asellus*), Reid 1944 (*Gammarus*),

Mann 1954 (leeches), and Ellis 1940, 1946, 1947, 1951, Macan 1949 (molluscs). Mr A. E. Ellis kindly checked my identifications of *Pisidium*.

Four collections were made in each locality at approximately three-monthly intervals. A round pond net was used for collecting in most areas; rooted vegetation, submerged timber, and stones were examined by hand. When a lot of decaying leaves, surface pond weed, or mud and fine debris was present, the material in the net was not picked over in the usual manner. Instead the material was washed, small amounts at a time, into a deep tray half filled with water, and then examined. Finally the tray was lowered into the water until just submerged, then raised and lowered alternately and at the same time gently rocked to and fro. As a result only the more dense material remained behind, together with any animals present (leeches, planorbids, *Sphaerium*, *Pisidium*). The time spent at each area of a locality was not constant, as collecting was continued until it was thought that no further species was likely to be found. The time taken to collect in each place was noted, and when the animals had been counted the appropriate factor was applied so that the numbers represented one hour's collecting. The figure that was finally taken to represent the abundance of a species in each locality was usually obtained by calculating the arithmetic mean of the figures recorded for each of the four collections. However, exceptionally high figures for abundance were obtained when collections were made following the breeding season of certain animals. These high values were disregarded when the final figures were calculated.

The abundance of animals was not estimated on a unit area basis because it was thought that since a square metre of reed bed represents a much greater surface area for attachment of animals than, for example, a square metre of stones, the results for two such habitats could be better compared if they were estimated on a time basis.

RESULTS

(*a*) *Chemical factors*

The seasonal fluctuations of all the factors measured are given in the Appendix. In general the highest values for total alkalinity were reached during the summer

Table 2. *Chemical data of the four ponds examined during July 1956*

	Potassium permanganate equivalent (p.p.m.)	Free ammonia (p.p.m.)	Albuminoid ammonia (p.p.m.)	Free ammonia as % of total alkalinity
Heath Pond	17·34	0·5	2·5	8·4
Hammond's	33·15	0·4	5·4	9·8
Leech	45·95	1·3	10·4	6·9
Egham	54·75	0·9	29·0	3·2

and early autumn, and the minimum values occurred during the winter months. In contrast, the maximum values for total hardness and calcium occurred during the winter, and the minimum values were reached during the summer and early

Table 3. *The fauna of the sixteen ponds expressed as the mean number of animals per hour's collecting, calculated as described in the text*

	Three Firs	Hammond's	Eagle	Gormoor	Heath Pond	Wasing	Heath Lake	Bagshot	Aldermaston	Chapel Row	Round Pound	Kiln Pond	Egham	Leech	Farley	Whiteknights
MOLLUSCA																
Acroloxus lacustris (Linn.)	–	–	–	–	–	–	–	–	–	–	–	–	–	9·9	22·4	9·8
Anodonta cygnea (Linn.)*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·4
Ancylus fluviatilis (Müller)	–	–	8·8	–	–	–	2·4	11·5	3·8	7·7	–	–	9·7	–	–	–
Bithynia tentaculata (Linn.)*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1·4
Potamopyrgus jenkinsi (Smith)*	–	–	–	–	–	–	–	–	–	–	–	0·8	–	–	–	–
Limnaea auricularia (Linn.)*	–	–	–	–	–	–	–	–	–	–	–	0·1	–	–	–	–
L. peregra (Müller)	–	–	41·6	–	–	–	10·1	0·8	0·5	2·2	–	2·0	–	–	–	0·4
L. stagnalis (Linn.)*	–	–	–	–	–	–	–	–	–	–	–	2·3	–	–	–	0·3
Pisidium casertanum (Poli.)	42·6	0·5	–	147·0	–	2·0	6·3	–	–	–	–	–	–	–	–	–
P. henslowanum (Sheppard)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
P. hibernicum Westerlund	–	–	–	–	–	–	–	26·8	–	–	–	15·7	–	–	–	–
P. milium Held	–	–	–	–	–	–	–	–	–	49·3	–	7·1	–	–	–	0·2
P. nitidum Jenyns	–	–	–	–	–	–	–	–	2·2	–	–	–	–	–	–	
P. obtusale (Lamarck)	2·8	4·2	37·0	–	–	–	–	–	3·7	–	7·0	–	–	113·1	–	–
P. pulchellum Jenyns	–	–	–	–	–	–	3·0	–	–	–	–	–	–	–	–	–
P. subtruncatum Malm.	–	–	–	–	–	–	2·4	21·8	–	–	–	18·7	–	–	–	–
Planorbarius corneus (Linn.)*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·5
Planorbis albus Müller	–	–	–	–	–	–	–	13·1	11·0	–	–	15·2	2·1	–	3·0	0·5
P. contortus (Linn.)	–	–	–	–	–	–	–	–	–	20·6	–	8·6	–	–	–	–
P. crista (Linn.)	–	–	8·6	–	–	–	–	–	–	17·1	–	–	9·2	–	15·6	0·4
P. leucostoma Millet	–	–	–	–	–	–	–	–	–	–	–	0·6	–	–	–	–
P. vortex (Linn.)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1·6
Segmentina complanata (Linn.)	–	–	–	–	–	–	–	0·8	–	–	2·4	1·7	27·1	25·2	156·3	0·4
Sphaerium lacustre (Müller)	–	–	2·2	–	–	–	0·4	–	0·5	3·5	–	–	11·4	–	–	0·2
HIRUDINEA																
Erpobdella octoculata (Linn.)	–	–	–	–	–	2·2	–	0·8	–	–	–	0·3	4·0	–	3·2	8·8
E. testacea Savigny	–	–	–	–	–	–	1·4	1·8	–	–	–	6·0	–	1·3	7·8	–
Glossiphonia complanata Linn.	–	–	–	–	–	–	–	1·3	–	–	–	0·7	–	–	3·0	–
G. heteroclita Linn.	–	–	–	–	–	–	–	0·2	–	–	–	–	6·7	4·4	1·7	2·5
Haemopis sanguisuga Linn.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·3	–
Helobdella stagnalis Linn.	–	–	5·8	–	–	0·2	–	5·5	–	6·2	–	1·2	11·9	8·3	33·9	11·5
Hemiclepsis marginata (Müller)*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·9
Piscicola geometra Linn.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0·3	–
Theromyzon tessulatum (Müller)*	–	–	–	–	–	–	–	–	–	–	–	–	–	0·5	0·7	0·2
TURBELLARIA																
Dendrocoelum lacteum (Müller)	–	–	–	–	–	1·9	–	–	–	–	–	1·9	–	2·1	4·2	2·9
Planaria lugubris (Schmidt)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3·9
Polycelis cornuta (Johnson)*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1·5
P. nigra (Ehrenb.)	–	–	–	–	15·9	0·2	–	–	–	0·8	–	1·5	6·9	1·1	16·5	7·8
CRUSTACEA																
Asellus aquaticus (Linn.)	–	–	–	–	–	–	–	7·8	–	–	–	–	–	–	–	28·4
A. meridianus Rac.	–	–	–	–	–	9·2	7·2	–	–	20·3	–	9·8	–	7·9	37·2	–
Gammarus pulex (Linn.)	–	–	–	–	–	–	–	0·4	–	–	–	0·3	–	–	–	10·0

An asterisk indicates that the species is omitted from further consideration for reasons given in the text.

(*Facing p. 108*)

autumn. No seasonal fluctuation of magnesium was apparent, and in most localities the concentrations varied erratically throughout the year. The values for dissolved organic matter throughout the summer of 1954 were high compared with those for the following winter. It seems likely that the high values recorded during the first few months of 1954 were associated with prolonged freezing. The lowest values for the pH of the water were usually recorded during the months December to March. The seasonal variation in the pH of the water was only slight in the hard-water localities, Farley and Whiteknights, apart from a few erratic fluctuations. On the whole, the pH of the sub-aquatic soil did not fluctuate as much as that of the water. With the exception of Wasing, the mean values for the pH of the water exceeded those of the sub-aquatic soil by about 0·6 unit. The results for the estimation of free and albuminoid ammonia in four ponds during July 1956 appear in Table 2.

(*b*) *The fauna*

Table 3 contains the mean numbers of animals per hour's collecting for each species. Those species marked with an asterisk have been excluded from further consideration since their distribution is known to be affected by factors such as the size of the basin and the availability of suitable food.

DISCUSSION

(*a*) *Inter-relationships of the chemical factors, and the effect of rainfall*

As progressively harder waters are considered, there is usually a corresponding increase in the mean values for total alkalinity (see Appendix). Also increasing mean calcium concentration is usually accompanied by a corresponding increase in the

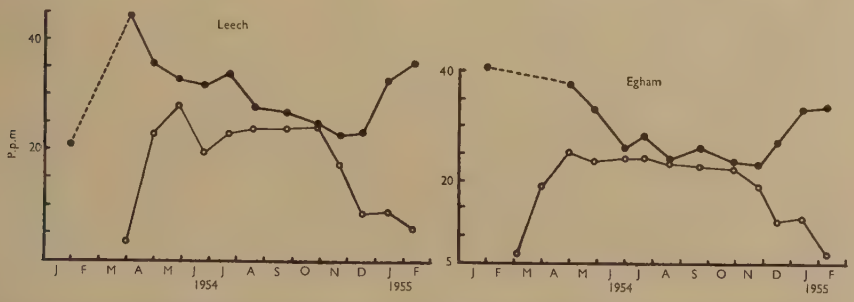

Fig. 1. Monthly estimates of calcium (●——●) and total alkalinity (O——O) from January 1954 to February 1955.

amount of variation in the total alkalinity throughout the year (as measured by the sum of the deviations of each value from the mean). In addition, a seasonal relationship appears to exist between calcium content and total alkalinity. The calcium value usually exceeds that of the total alkalinity, and the difference between them is greatest during the winter and least during the summer and early

autumn. This tendency is particularly well illustrated in Leech and Egham (see Fig. 1). In Table 4 the localities are arranged in order of increasing mean dissolved organic matter, and figures are given to show the difference between calcium content and total alkalinity in each locality at times of the year when the two factors are most similar (October 1954) and dissimilar (February 1955). The differences between the two sets of values are listed in a third column. The space between Three Firs and Whiteknights separates the ponds into two distinct groups. The means in the third column show that the total alkalinity deviates most markedly from the calcium values in the latter group, those with most dissolved organic

Table 4. *The relation between calcium and total alkalinity at times of the year when the factors are most similar and dissimilar*

Ponds are arranged in order of increasing mean dissolved organic matter. For further details, see text.

	Calcium minus total alkalinity		October difference minus February difference
	October	February	
Heath Pond	7·4	8·0	0·6
Heath Lake	4·0	12·6	8·6
Wasing	4·9	9·9	5·0
Gormoor	2·4	6·2	3·8
Aldermaston	3·6	6·2	2·6
Hammond's	0·9	6·4	5·5
Bagshot	3·5	10·4	6·9
Round Pond	3·6*	13·9	10·3
Three Firs	−0·3	6·3	6·6
			Mean 5·5
Whiteknights	22·3	53·3	31·0
Farley	5·7	23·8	18·1
Kiln Pond	6·6	11·2	4·6
Eagle	0·0	2·2	2·2
Leech	1·3	30·1	28·8
Egham	1·5	27·0	25·5
Chapel Row	−4·6	1·5	6·1
			Mean 16·6

* September value; as October value was abnormally high.

matter. Most of these localities contain hard water except Chapel Row and Eagle, which are also exceptional amongst the soft-water ponds in having particularly high total alkalinity values. In addition to its relation to dissolved organic matter, the degree of fluctuation appears to be governed to some extent by the size of the water basin, and inflowing streams; *e.g.* compare Round Pond, Three Firs and Kiln Pond. Calcium and total hardness fluctuate more or less together throughout the seasons. Thus the relation between total hardness and total alkalinity is similar to, though less clearly defined than, the relationship between calcium and total alkalinity.

The degree of fluctuation in concentration of dissolved organic matter in closed ponds is related to the volume of water in the basin. This is demonstrated in

Table 5, where these localities are arranged in order of increasing mean volume. When the sums of the deviations from the means of each set of values are studied in relation to the volume of water in each locality, it is found that the deviations

Table 5. *Closed localities arranged in order of increasing volume*

The space separates smaller ponds (<120 cu. ft $\times 10^3$) from the larger.

	Volume ($ft^3 \times 10^3$)	Sum of the deviations of each value from the mean values for dissolved organic matter	
Chapel Row	3·45	195	
Round Pond	5·96	115	
Farley	17·96	109	
Eagle	19·40	99	Mean value, 151·5
Three Firs	30·27	144	
Egham	84·35	317	
Aldermaston	85·37	93	
Leech	112·86	140	
Heath Lake	254·83	45	
Hammond's	299·59	65	Mean value, 50·8
Heath Pond	439·05	49	
Wasing	563·60	44	

are least in the larger ponds. It follows that the volume of water in a pond has an important bearing upon the fluctuations in concentration of dissolved organic matter throughout the year.

Three Firs is the only locality in which a direct relation between the seasonal fluctuations in the colour (brownness) values and dissolved organic matter is clearly

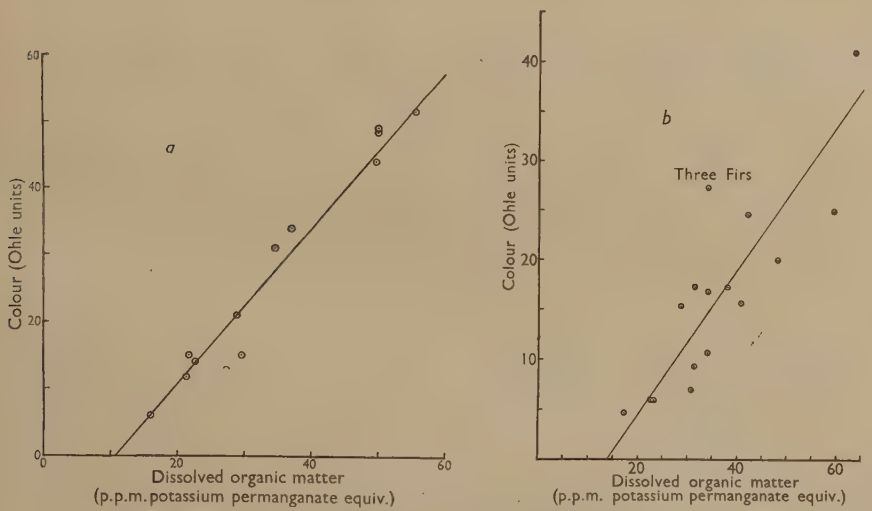

Fig. 2. The relation between colour and mean dissolved organic matter: *a*, in Three Firs, between February 1954 and February 1955; *b*, in the sixteen localities.

shown (Fig. 2*a*). In all localities, however, the mean colour of the water is approximately proportional to the mean amount of dissolved organic matter present. The point representing Three Firs in Fig. 2*b* stands well apart from the others. The reason for this may be linked with the fact that Three Firs is a closed, peaty pond and the substances being matched by methyl orange in the colour estimation are different in nature from those in most other ponds.

It appears from Fig. 3 that as more alkaline waters are considered the pH of the water rises with total alkalinity up to 7·0 p.p.m. In more alkaline waters the pH is more variable, but the mean value is nowhere less than 6·7. In hard waters the pH of the water is remarkably uniform throughout the year, but in softer waters the pH and total alkalinity generally rise and fall together. In very small basins (Chapel Row, Round Pond), however, erratic fluctuations were observed.

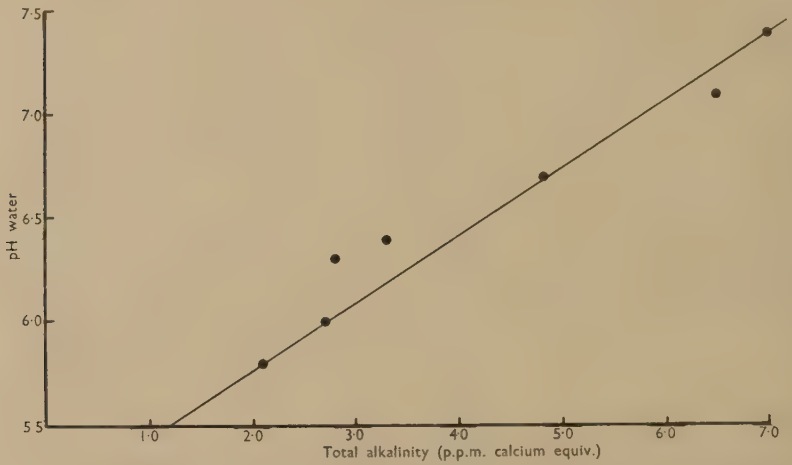

Fig. 3. The relation between mean pH water and mean total alkalinity in seven localities having a mean total alkalinity less than 7·0 p.p.m.

It will be gathered from the preceding paragraphs that calcium is the basic factor in determining the overall chemical nature of the ponds. Thus, a locality which has a high concentration of calcium may be expected to have a high, stable pH, and high total alkalinity and dissolved organic matter values. Localities which show anomalous features are usually found to have abnormally high concentrations of dissolved organic matter, and to be exceptionally small basins.

The effect of rainfall is difficult to trace from the present data, as samples were taken at approximately regular intervals irrespective of the weather conditions. Moreover, rainfall figures are available only for the Reading area, whereas the ponds are scattered over a wide area around Reading. It is likely that local variation in rainfall has a considerable effect upon the chemical composition of the water in small ponds. However, Chapel Row is a small pond only 10 miles from Reading and the seasonal fluctuations here may be considered in relation to

the figures for rainfall at Reading. Although few of the variations shown in Fig. 4 can be related to the amount of rainfall, all values decreased following periods of heavy rainfall during May and June, and during November. Clearly, other factors need to be considered and of these the amount of biological activity may be of considerable importance. This aspect is considered later.

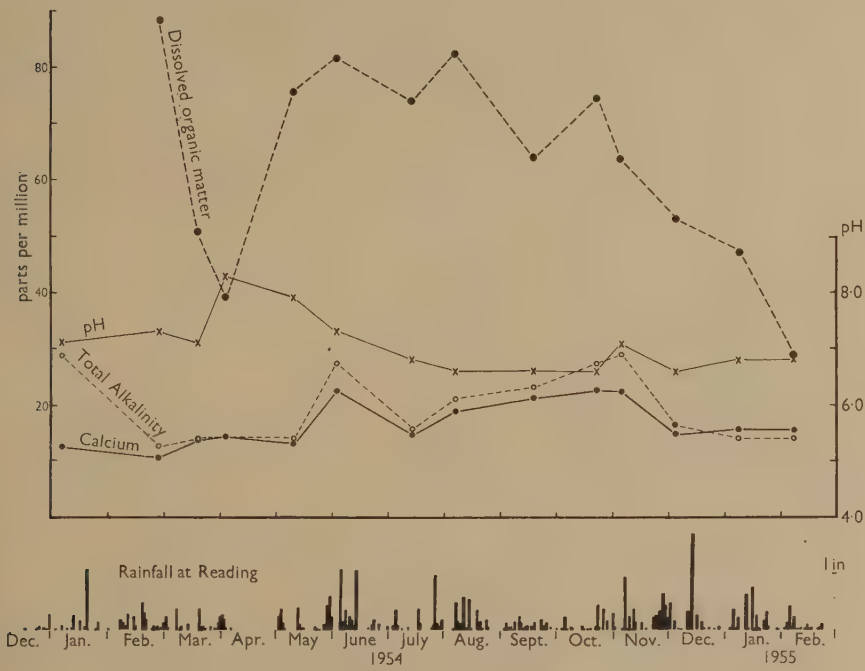

Fig. 4. Fluctuations in four chemical factors in Chapel Row in relation to rainfall.

The extent of the annual fluctuations is such that it is essential that the seasonal variations throughout at least one year are known before comparison between the fauna of the various ponds in relation to the chemistry of the water can be seriously attempted.

(b) Relation between the soft-bodied fauna and chemical conditions

It is found that the numbers of both species and individuals are relatively high in those ponds containing 25 p.p.m. of calcium (Table 6). In progressively softer waters there are in general fewer and fewer species, and the animals are less numerous. These observations are in agreement with those of previous workers (Ohle 1934, Boycott 1936, Mann 1955) who similarly found that waters containing less than 25 p.p.m. of calcium do not support the variety and abundance of soft-bodied animals commonly associated with harder waters. The exceptions to this

general pattern are usually associated with high concentrations of dissolved organic matter.

Although the precise reaction which takes place when the water is boiled with potassium permanganate is not known, it is generally assumed that the values obtained indicate approximately the amount of oxidizable organic matter present in solution. For convenience the values for this estimation are referred to as dissolved organic matter. In Fig. 5 the points have been plotted to represent the calcium content and the dissolved organic matter in each locality, and against each point is recorded the number of species, followed by the number of animals per

Table 6. *The fauna in relation to the chemistry of the water*

	Mean calcium concentration (p.p.m.)	Mean dissolved organic matter (p.p.m.)	Number of species	Abundance of animals
Three Firs	6·3	34·2	2	44
Hammond's	7·7	31·1	2	5
Eagle	8·4	42·2	6	104
Gormoor	8·6	28·9	1	147
Heath Pond	8·7	17·3	1	16
Wasing	10·2	23·1	6	16
Heath Lake	12·2	22·5	8	33
Bagshot	14·7	31·3	13	93
Aldermaston	16·2	30·5	6	22
Chapel Row	16·6	63·2	8	120
Round Pond	16·9	33·7	3	17
Kiln Pond	27·3	40·9	16	91
Egham	28·5	59·1	9	89
Leech	30·5	47·9	9	173
Farley	45·4	38·2	12	305
Whiteknights	88·3	34·3	17	81

hour's collecting. Points in the same part of the diagram have approximately the same richness of fauna. Thus, Heath Pond, Gormoor, Hammond's and Three Firs, which have soft water and little dissolved organic matter, contain few species and few animals, except in Gormoor where a single species of *Pisidium* flourished exceedingly. On the other hand Whiteknights, Farley, Kiln Pond, Leech and Egham, which have hard water and a high content of dissolved organic matter, yielded nine or more abundant species. The remaining localities, in the intermediate range of calcium concentration, have varying numbers of species and individuals, but greater abundance is in general associated with higher values for dissolved organic matter.

If one attempts to relate this picture to the conventional classification into oligotrophic, eutrophic and dystrophic, the group in the upper right-hand corner of the diagram would clearly be eutrophic, assuming that the abundance of the soft-bodied animals reflects the total productivity of the habitat. The group of ponds in the bottom left-hand corner of the diagram would seem to be oligotrophic or dystrophic and the remainder fall somewhere between the two. It is characteristic of dystrophic localities (Strøm 1928) that peaty material accumulates,

and this might be expected to be reflected in the dissolved organic matter and colour estimations. This probably explains why Gormoor, Hammond's and Three Firs have fewer species than Heath Lake and Wasing. The former group might be regarded as the dystrophic localities and the latter as oligotrophic. Thus the dissolved organic matter determinations as well as those of calcium, are of considerable value in assessing the suitability of a locality for soft-bodied animals.

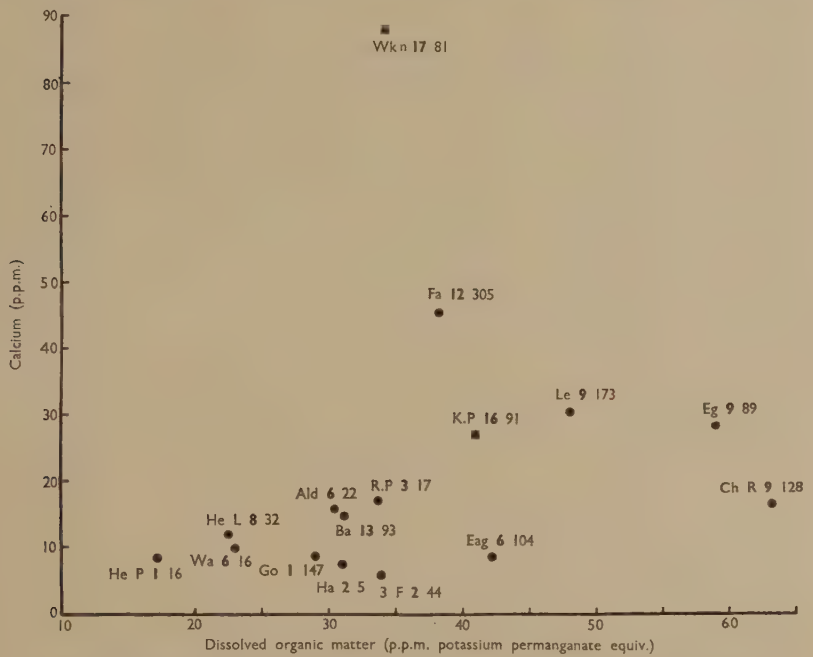

Fig. 5. Localities plotted according to mean calcium content and mean dissolved organic matter. The number of species present is shown in heavy type, followed by the number of animals per hour's collecting.

Key to localities:

3F, Three Firs	Ha, Hammond's	Eag, Eagle
Go, Gormoor	He P, Heath Pond	Wa, Wasing
He L, Heath Lake	Ba, Bagshot	Ald, Aldermaston
Ch R, Chapel Row	R.P, Round Pond	K.P, Kiln Pond
Eg, Egham	Le, Leech	Fa, Farley
Wkn, Whiteknights		

When the fauna contained in the soft-water ponds is compared with records taken from lakes containing similar or even smaller amounts of calcium, it is found that several species occurring in the latter localities are absent from the soft-water ponds. For instance *Asellus aquaticus, Gammarus pulex, Dendrocoelum lacteum, Planaria lugubris, Erpobdella octoculata, Glossiphonia complanata,* and several species of mollusc occur in Windermere (Moon 1936, Macan 1950, Mann 1955) which contains only approximately 5·0 p.p.m. of calcium. Similarly, Hunter (1953) records the occurrence of several species of mollusc in Loch Lomond

(which contains 2·3 to 3·3 p.p.m. of calcium). With regard to fresh-water molluscs, Boycott (1936) and Macan (1950) have shown that the large size of a locality can be a compensating factor in the distribution of molluscs in soft waters, and this seems to be the case also with a number of other animals. One possible explanation for this is that humic acids do not develop and accumulate to the same extent in large bodies of water as in small localities, and it may be that in the latter case the concentration of humic acids is unfavourable to many soft-bodied or shelled animals.

A simple experiment to test the effect of humic acids on flatworms has been carried out. The species used in the experiment was *Dendrocoelum lacteum*, and a supply of peaty water was obtained from a tarn in the Lake District. Five experimental solutions were used, one of them being the natural peaty water. The other solutions were prepared by diluting the original water with distilled water so as to obtain waters containing dissolved organic matter in the order of $\frac{2}{3}$, $\frac{1}{2}$, $\frac{1}{4}$ and $\frac{1}{8}$ of the concentration of the original medium. The calcium concentration was maintained at the original level (2·2 p.p.m.) by adding calcium bicarbonate solution. The chemical data for the various solutions are given in Table 7. The worms were collected four days before the experiment was commenced, and were

Table 7. *Results of the experiment, and chemical data of the solutions used*

Solution I contains normal peaty water; solutions II to V are dilutions of this water, as indicated.

	Solution number				
	I	II	III	IV	V
Ratio, peaty water to distilled water	1:0	2:1	1:1	1:3	1:7
Dissolved organic matter (p.p.m.)	152·74	100·0	75·0	37·5	18·8
Colour (Ohle units)	119·5	85·0	66·0	23·0	10·5
pH	3·77	4·02	4·00	4·81	6·22
Time to 100% loss of adhesion (h)	$\frac{1}{4}$	$2\frac{3}{4}$	$6\frac{1}{2}$	∞	∞
Time to 100% mortality (h)	6	$8\frac{1}{2}$	12	∞	∞

all of about the same size. The specimens were arranged in five groups corresponding to the five experimental solutions, and each group contained four worms. These were placed separately in small glass dishes, each of which contained approximately 50 ml of water. The water in each dish was changed every 12 h, and replaced with freshly-aerated water. The specimens were examined at half-hourly intervals for the first 12 h of the experiment, and their general behaviour was observed. Two conditions were noted in particular, loss of power of adhesion and time of death. The latter condition was assumed when there was no response to stimulation. It was found that the worms in the two more dilute solutions survived for many hours (at least 120 h, after which observations were no longer made) without showing any signs of serious disturbance. On the other hand, the specimens placed in the three more concentrated solutions showed an immediate reaction to the waters and all died within 12 h.

(c) Seasonal fluctuations of calcium and total alkalinity in relation to the concentration of dissolved organic matter and the fauna

It has already been shown that in general the calcium concentration of pond water increases throughout the autumn and decreases throughout the spring and early summer, so that the maximum and minimum values occur during the winter and late summer respectively. The fluctuations of total alkalinity show the reverse effect, and the degree of fluctuation of both these factors is most marked in ponds containing high concentrations of dissolved organic matter. It will be noted that all the ponds at the lower end of Table 4, which show the most marked fluctuations, lie to the right-hand side in Fig. 5, and are regarded as productive localities.

Thus it seems likely that high productivity in small bodies of water is associated with certain characteristics in the chemistry of the water. A productive pond may be expected to contain a high concentration of dissolved organic matter (potassium permanganate equivalent 30 p.p.m. and over), and to show wide seasonal fluctuations in concentration of calcium and in total alkalinity. The fall in calcium content during the summer might be explained by the precipitation of calcium carbonate by plants during the period of maximum photosynthetic activity throughout the summer months, but this explanation does not fit the observed rise in total alkalinity at the same time of year, because precipitation of calcium carbonate would inevitably lead to a fall in the amount of titrateable base in solution. A second explanation that has been considered is that the rise in total alkalinity might be due to an increase in concentration of free ammonia liberated by organic decay. This has been rejected because it was shown that free ammonia accounted for not more than 10% of the total alkalinity in four ponds which were examined during July 1956 (Table 2). An alternative explanation has been suggested by Mr F. J. H. Mackereth, of the Freshwater Biological Association, Windermere. It is that in the early part of the year the calcium ions in the water are balanced by some anion other than HCO_3^-, which means that the calcium is not present as bicarbonate, carbonate, or hydroxide. It might be balanced by chloride or by sulphate ions, and of these the latter seem the more likely. Assuming, therefore, that the calcium is present as calcium sulphate at the beginning of the year, the rise in alkalinity during the summer could be due to the reduction of $SO_4^=$ on the mud surface to $S^=$, which is then locked up in the mud as ferrous sulphide. The $SO_4^=$ is replaced by HCO_3^-, produced by the decomposition of organic material in the mud. Thus, the net effect is the replacement of $SO_4^=$ by HCO_3^-, and this causes a rise in the alkalinity. This process may be accompanied by some loss of calcium as calcium carbonate, which may account for the overall loss of calcium in the summer. During the autumn reoxygenation of the ferrous sulphide produces sulphuric acid which reacts with calcium bicarbonate to re-form calcium sulphate with the evolution of carbon dioxide, which is lost to the atmosphere. This brings about a fall in alkalinity, and the action of sulphuric acid on the calcium carbonate in the mud may lead to an increase in calcium concentration. If this explanation is correct, one would expect the $SO_4^=$ content of the water to

be high in the winter and low during the summer. This has recently been found to be the case in Heath Pond, Hammond's, Leech and Egham (Dr K. H. Mann, personal communication). On this hypothesis one would expect that the fluctuation would be most marked in ponds where the reducing action of the mud is greatest, *i.e.* where the greatest amount of organic material is present in conditions which favour bacterial decay. This correlation would then explain the link between the seasonal fluctuation of calcium and total alkalinity, and the productivity of the ponds.

ACKNOWLEDGMENTS

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SUMMARY

1. Variations in total hardness, total alkalinity, concentration of calcium and magnesium, colour, dissolved organic matter, and the pH of the water and of the sub-aquatic soil have been recorded in sixteen ponds throughout a period of 14 months.

2. Most of the inter-relationships between the chemical factors are related to the calcium content of the water.

3. Seasonal fluctuations in calcium and total alkalinity occur in all the ponds studied. The degree of fluctuation is related to the concentration of dissolved organic matter in the water. The fluctuation is greatest in hard waters and certain small localities containing softer water.

4. The colour (measured as brownness) of the water is roughly proportional to the dissolved organic matter content, though a seasonal relationship between these two factors has only been found in one small, dystrophic pond.

5. Erratic fluctuations occur most commonly in small bodies of water.

6. Collecting was confined to molluscs, leeches, flatworms and *Gammarus* and *Asellus*. The more important factors influencing the total numbers of animals present are shown to be calcium concentration, size of basin and concentration of dissolved organic matter. Few species are present in dystrophic localities, *i.e.* those with low calcium values and high colour and dissolved organic matter values. More species are found in oligotrophic localities, characterized by low calcium, colour and dissolved organic matter values. The hard, eutrophic waters have a high content of dissolved organic matter and are rich in species and numbers of animals.

7. It is suggested that one reason why so few animals occur in the soft-water ponds compared with larger bodies of water containing smaller amounts of calcium is that the concentration of humic acids tends to be much greater in the small basins.

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APPENDIX

Chemical determinations

The sixteen ponds are arranged in order of increasing calcium concentration. Maxima are shown in bold, minima in italic figures. Parentheses indicate an element of doubt about the accuracy of certain figures.

Total alkalinity (p.p.m. calcium equiv.)

	1954												1955		Max.	Min.	Mean	Sum of deviations
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.				
Three Firs	**8·8**	5·6	4·0	3·4	1·8	6·2	5·6	6·4	6·6	6·8	5·4	3·4	*1·4*	1·8	**8·8**	*1·4*	4·8	26·0
Hammond's	3·2	2·8	3·4	3·6	**4·0**	3·0	2·2	**4·0**	3·6	3·6	2·4	1·8	2·2	*1·0*	**4·0**	*1·0*	2·8	10·4
Eagle	11·4	12·0	11·4	5·5	**13·6**	10·8	7·6	7·8	8·8	10·4	9·6	6·4	*4·6*	5·6	**13·6**	*4·6*	9·0	32·9
Gormoor	3·2	2·4	2·7	2·8	2·6	3·2	1·6	3·2	3·2	**4·4**	2·8	2·0	*1·4*	1·8	**4·4**	*1·4*	2·7	8·3
Heath Pond	3·0	**3·2**	2·6	1·2	2·2	1·8	2·2	2·6	2·4	2·0	1·6	2·0	1·2	*1·0*	**3·2**	*1·0*	2·1	7·4
Wasing	(**7·2**)	3·2	2·2	2·8	2·4	2·6	*1·8*	3·2	4·6	3·8	3·6	4·0	2·4	1·8	**7·2**	*1·8*	3·3	14·0
Heath Lake	9·0	7·2	7·4	*3·5*	6·6	5·9	7·0	8·8	**9·8**	8·0	8·0	7·2	4·4	4·8	**9·8**	*3·5*	7·0	19·3
Bagshot	6·4	5·6	6·4	6·6	6·6	7·0	**7·6**	7·2	7·2	6·8	6·2	6·4	6·0	*5·2*	**7·6**	*5·2*	6·5	6·8
Aldermaston	12·4	11·6	**13·2**	9·8	10·4	11·6	10·0	12·8	11·2	13·2	12·2	11·4	*9·4*	10·4	**13·2**	*9·4*	11·4	15·4
Chapel Row	28·8	*12·8*	13·8	14·2	14·0	27·6	15·6	21·2	23·4	27·4	**29·0**	16·4	14·0	14·0	**29·0**	*12·8*	19·5	82·6
Round Pond	–	–	6·4	6·8	7·2	12·8	12·8	13·2	9·8	**18·8**	11·2	*5·2*	5·6	6·4	**18·8**	*5·2*	9·6	45·6
Kiln Pond	23·2	16·4	14·0	15·6	15·6	21·4	20·0	24·0	27·2	**29·2**	24·6	*13·9*	14·2	14·0	**29·2**	*13·9*	19·5	65·9
Egham	–	*6·4*	18·8	**24·8**	23·6	24·0	24·0	23·2	22·4	22·0	19·2	12·6	13·2	6·6	**24·8**	*6·4*	18·5	77·2
Leech	–	–	*3·6*	22·8	**28·1**	19·4	22·8	23·9	24·0	24·0	17·6	8·2	9·0	6·2	**28·1**	*3·6*	17·5	98·7
Farley	49·6	29·6	27·2	28·0	**50·4**	40·0	42·4	39·6	37·0	43·8	38·0	21·2	22·4	*21·0*	**50·4**	*21·0*	35·0	121·4
Whiteknights	**62·6**	49·2	46·8	43·6	51·2	52·0	53·4	59·6	62·0	61·2	58·8	42·5	*34·0*	38·2	**62·6**	*34·0*	51·1	104·3

Total hardness (p.p.m.)

Three Firs	*7·4*	10·9	**11·8**	11·7	11·4	11·7	11·8	9·2	9·6	10·6	8·7	10·1	**15·0**	14·6	**15·0**	*7·4*	11·0	21·5
Hammond's	9·0	**12·6**	**12·6**	9·5	10·4	9·5	7·7	7·0	*6·0*	6·7	7·9	10·6	11·5	8·6	**12·6**	*6·0*	9·3	23·8
Eagle	11·2	11·5	11·8	12·0	14·0	12·4	*9·3*	10·6	11·6	**14·3**	12·9	10·7	10·1	11·4	**14·3**	*9·3*	11·7	14·4
Gormoor	10·6	**16·5**	12·6	11·6	10·8	11·2	*8·4*	9·8	9·3	8·7	11·3	12·1	12·1	12·0	**16·5**	*8·4*	11·2	19·4
Heath Pond	*13·1*	15·5	16·0	16·8	17·3	16·9	16·2	15·9	16·3	17·6	16·9	16·3	**17·8**	17·1	**17·8**	*13·1*	16·4	11·1
Wasing	*14·3*	17·9	13·5	18·0	15·9	15·5	17·0	16·4	15·0	15·3	14·5	**21·8**	19·0	18·9	**21·8**	*14·3*	16·6	25·4
Heath Lake	17·9	*17·1*	18·5	18·4	18·7	17·5	19·8	19·8	20·1	20·5	19·0	21·8	22·4	**27·0**	**27·0**	*17·1*	19·9	24·7
Bagshot	16·8	20·9	18·6	14·9	16·7	19·5	14·7	17·2	*14·3*	14·4	20·7	22·1	**22·3**	22·1	**22·3**	*14·3*	18·2	37·2
Aldermaston	*17·0*	17·8	17·6	17·5	17·6	19·4	19·5	19·3	19·4	19·5	18·9	**20·8**	18·7	18·3	**20·8**	*17·0*	18·7	12·3
Chapel Row	43·3	*13·5*	15·3	15·4	14·2	26·6	16·0	21·0	24·3	**27·3**	26·5	18·4	19·0	17·9	**27·3**	*13·5*	19·6	59·0
Round Pond	–	*14·6*	25·1	26·4	25·7	25·8	22·6	20·6	20·8	27·2	21·5	25·2	**31·5**	31·4	**31·5**	*14·6*	24·5	47·7
Kiln Pond	31·4	32·7	28·8	28·7	28·3	30·4	31·2	33·3	33·3	40·7	41·7	35·3	32·0	32·3	**41·7**	*28·3*	32·9	40·1
Egham	–	(*12·9*)	37·1	**44·0**	36·3	32·6	34·2	31·3	32·2	30·6	29·2	33·0	37·5	43·0	**44·0**	*12·9*	34·3	80·6
Leech	–	*31·0*	**58·0**	36·9	33·1	33·2	**36·2**	34·4	32·9	31·9	29·8	33·7	43·4	43·7	**58·0**	*31·0*	36·2	51·5
Farley	52·9	50·8	52·4	51·8	**56·8**	50·3	47·5	47·5	48·0	56·3	53·0	*42·8*	46·5	44·8	**56·8**	*42·8*	50·1	47·0
Whiteknights	90·6	91·8	99·0	84·5	**106·8**	100·3	91·5	89·6	90·4	88·0	88·5	*83·0*	91·8	97·5	**106·8**	*83·0*	92·4	67·3

Calcium (*p.p.m.*)

	1954												1955					
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Max.	Min.	Mean	Sum of deviations
Three Firs	*3·0*	7·0	6·9	6·6	**6·5**	7·2	7·2	5·5	5·5	6·5	5·0	6·0	6·7	**8·1**	**8·1**	*3·0*	6·3	12·3
Hammond's	6·4	10·3	**10·6**	8·5	9·3	8·3	6·9	5·6	5·4	*4·5*	4·9	8·9	10·2	7·4	**10·6**	*4·5*	7·7	25·0
Eagle	*6·5*	19·5	8·4	8·8	9·3	8·7	6·8	7·8	8·4	**10·4**	9·3	7·8	7·5	7·8	**10·4**	*6·5*	8·4	11·8
Gormoor	**6·5**	**13·8**	9·8	9·0	8·3	8·9	*6·2*	7·6	8·2	6·8	8·3	9·9	9·2	8·0	**13·8**	*6·2*	8·6	17·9
Heath Pond	*4·6*	9·3	8·4	8·9	9·4	9·1	8·5	8·3	8·9	9·4	8·9	8·8	**10·1**	9·0	**10·1**	*4·6*	8·7	9·8
Wasing	7·7	11·5	*7·3*	11·2	9·9	9·7	10·5	10·0	8·6	8·7	8·5	**15·1**	12·0	11·7	**15·1**	*7·3*	10·2	22·1
Heath Lake	*9·2*	12·8	10·9	11·2	11·0	10·2	11·6	11·7	12·1	12·0	10·9	13·7	16·2	**17·4**	**17·4**	*9·2*	12·2	50·0
Bagshot	10·9	15·9	15·6	13·2	13·9	15·8	11·8	14·3	12·5	*10·7*	18·0	18·2	**18·5**	16·4	**18·5**	*10·7*	14·7	31·8
Aldermaston	*12·7*	14·2	15·2	14·8	15·4	16·9	17·8	17·4	17·4	16·8	15·8	**18·9**	16·8	16·6	**18·9**	*12·7*	16·2	18·1
Chapel Row	12·5	*10·5*	13·7	14·2	13·0	22·6	14·5	18·8	21·2	**22·8**	22·6	14·9	15·6	15·5	**22·8**	*10·5*	16·6	50·0
Round Pond	*12·3*	–	**23·7**	18·1	17·3	17·2	17·0	12·4	13·4	16·4	13·3	17·4	21·5	20·3	**23·7**	*12·3*	16·9	36·6
Kiln Pond	*22·2*	26·3	23·4	23·2	23·8	25·6	25·9	28·4	30·7	35·8	**37·1**	29·3	24·9	25·2	**37·1**	*22·2*	27·3	50·0
Egham	(41·0)	–	–	**37·4**	32·9	25·8	27·8	23·7	25·8	23·5	*22·9*	27·0	32·8	33·6	**37·4**	*22·9*	28·5	47·7
Leech	*21·3*	–	**44·6**	36·3	32·8	31·9	34·2	27·8	27·0	25·3	23·0	23·5	33·0	36·3	**44·6**	*21·3*	30·5	75·7
Farley	38·4	50·4	49·7	49·1	**52·1**	45·4	45·7	46·4	48·3	49·5	43·8	*33·9*	38·3	44·0	**52·1**	*33·9*	45·4	55·8
Whiteknights	*75·2*	90·0	95·0	83·8	**100·9**	97·5	90·9	87·8	87·0	83·5	83·8	79·8	90·1	91·5	**100·9**	*75·2*	88·3	75·0

Magnesium (*p.p.m.*)

Three Firs	2·7	2·4	3·0	**3·1**	3·0	2·8	2·7	2·3	2·5	2·5	*2·2*	2·5	5·0	4·0	**3·1**	*2·2*	2·9	7·1
Hammond's	1·6	1·4	1·3	0·6	0·7	0·7	0·5	0·8	*0·4*	1·3	**1·8**	1·0	0·9	1·7	**1·8**	*0·4*	1·0	5·1
Eagle	**2·9**	*1·2*	2·1	2·0	2·9	2·3	1·5	1·7	2·0	2·3	2·2	1·8	1·6	2·2	**2·9**	*1·2*	2·1	5·1
Gormoor	**2·5**	1·7	1·7	1·6	1·5	1·4	1·3	1·3	*0·6*	1·2	1·9	1·3	1·7	2·5	**2·5**	*0·6*	1·6	5·0
Heath Pond	**5·2**	*3·8*	4·6	4·8	4·8	4·7	4·7	4·6	4·5	5·0	4·9	4·5	4·7	5·0	**5·2**	*3·8*	4·7	3·0
Wasing	4·0	3·9	3·8	4·1	*3·4*	3·5	4·0	3·9	3·9	4·0	3·7	3·4	4·2	**4·4**	**4·4**	*3·4*	3·9	2·9
Heath Lake	5·3	*2·7*	4·7	4·4	4·7	4·4	5·0	4·9	5·2	4·4	4·9	4·4	3·8	**5·9**	**5·9**	*2·7*	4·7	7·6
Bagshot	**3·6**	3·1	1·8	*1·0*	1·7	2·3	1·8	1·7	1·1	2·2	1·7	2·3	2·3	3·4	**3·6**	*1·0*	2·1	7·4
Aldermaston	**2·6**	2·2	1·5	1·7	1·3	1·5	*1·0*	1·1	1·2	1·6	1·9	1·2	1·2	1·1	**2·6**	*1·0*	1·5	4·9
Chapel Row	–	1·8	1·0	*0·7*	0·8	2·4	1·0	1·3	1·9	**2·7**	2·4	2·1	2·1	1·5	**2·7**	*0·7*	1·7	8·0
Round Pond	–	–	(0·8)	5·1	5·1	5·2	*3·4*	5·0	4·5	6·6	5·0	4·8	5·5	**6·8**	**6·8**	*3·4*	5·2	8·6
Kiln Pond	(5·6)	(3·9)	(7·4)	3·3	2·7	2·9	3·2	3·0	*1·5*	3·0	2·8	3·7	**4·3**	**4·3**	**4·3**	*1·5*	3·2	6·6
Egham	–	–	–	4·0	*2·1*	4·1	3·9	4·6	4·2	4·3	4·0	3·7	2·9	**5·8**	**5·8**	*2·1*	4·0	8·2
Leech	–	–	(8·2)	0·3	*0·2*	0·8	1·0	4·0	3·6	4·0	4·1	6·3	**6·4**	4·5	**6·4**	*0·2*	3·2	21·3
Farley	(8·8)	(0·2)	1·6	1·6	2·8	1·3	1·1	*1·0*	1·2	4·1	**5·6**	5·4	5·0	4·8	**5·6**	*1·0*	3·1	25·3
Whiteknights	(9·5)	1·1	2·1	0·5	3·6	1·7	*0·4*	1·1	2·1	2·7	2·9	2·1	1·0	**3·7**	**3·7**	*0·4*	1·9	12·3

Dissolved organic matter (p.p.m. potassium permanganate equiv.)

	1954										1955		Max.	Min.	Mean	Sum of deviations
	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.				
Three Firs	21·5	21·4	27·4	29·6	34·8	49·6	50·0	**55·8**	50·0	37·0	29·0	22·6	*16·1*	**55·8**	*16·1*	34·2	144
Hammond's	25·0	36·4	39·6	**46·3**	30·9	32·3	29·4	30·6	*22·3*	33·7	27·9	24·9	25·3	**46·3**	*22·3*	31·1	210
Eagle	**68·8**	46·1	36·4	46·2	41·6	48·9	45·6	45·5	59·5	43·3	41·7	29·1	*28·7*	**68·8**	*28·7*	42·2	99
Gormoor	23·5	33·9	25·2	*17·2*	37·2	26·8	33·9	**42·6**	34·3	26·4	21·9	23·8	29·1	**42·6**	*17·2*	28·9	75
Heath Pond	**24·9**	22·9	23·4	22·8	*11·4*	15·8	12·3	15·4	14·2	13·9	13·8	17·4	16·5	**24·9**	*11·4*	17·3	49
Wasing	23·5	25·6	25·9	19·2	*16·0*	24·8	**30·2**	26·4	19·5	17·6	26·6	22·5	22·2	**30·2**	*16·0*	23·1	44
Heath Lake	19·9	24·4	26·7	24·0	26·5	**28·2**	20·2	27·1	20·1	16·9	*15·6*	20·3	22·2	**28·2**	*15·6*	22·5	45
Bagshot	27·2	31·1	30·5	26·0	**60·6**	25·2	27·9	30·3	*23·1*	29·3	41·1	28·3	26·8	**60·6**	*23·1*	31·3	75
Aldermaston	**67·4**	38·0	29·5	24·8	24·6	25·6	26·2	31·5	30·4	27·9	*21·6*	23·3	25·3	**67·4**	*21·6*	30·5	93
Chapel Row	**88·2**	50·8	38·8	75·3	81·4	73·8	82·4	64·1	74·5	63·8	52·8	47·2	*28·7*	**88·2**	*28·7*	63·2	195
Round Pond	**218·6**	75·3	33·8	28·7	32·4	43·4	32·5	34·4	35·1	23·0	*12·1*	29·3	24·5	**218·6**	*12·1*	33·7	115
Kiln Pond	60·5	**65·4**	50·7	26·2	32·6	35·8	44·4	49·0	41·9	37·0	25·9	39·6	*23·3*	**65·4**	*23·3*	40·9	132
Egham	89·7	86·5	**118·6**	59·0	74·9	86·3	61·4	41·9	40·3	27·1	*25·6*	28·2	28·7	**118·6**	*25·6*	59·1	317
Leech	**295·4**	78·0	56·3	43·5	40·7	47·8	44·5	44·1	50·0	*26·4*	34·7	36·7	71·9	**295·4**	*26·4*	47·9	140
Farley	32·2	**60·0**	36·1	56·1	39·0	41·5	43·0	38·9	43·1	30·8	28·3	24·0	*23·7*	**60·0**	*23·7*	38·2	109
Whiteknights	32·5	39·6	37·6	**51·1**	30·7	37·4	33·5	42·9	29·4	27·9	27·0	29·7	*26·0*	**51·1**	*26·0*	34·3	83

Colour (Ohle units)

Three Firs	15·0	11·5	12·5	15·0	31·0	44·0	49·0	**55·0**	48·5	34·0	21·0	14·0	*6·0*	**55·0**	*6·0*	27·4	199·5
Hammond's	6·5	*6·0*	6·5	11·0	7·0	9·5	8·5	8·5	7·5	9·0	12·0	13·0	**15·0**	**15·0**	*6·0*	9·2	28·6
Eagle	17·5	18·0	*11·0*	11·5	19·0	25·0	26·0	28·0	35·5	**36·0**	35·0	24·5	24·0	**36·0**	*11·0*	23·9	85·3
Gormoor	*7·0*	7·5	*7·0*	8·5	11·0	12·0	21·0	22·5	**28·0**	24·5	10·0	18·0	20·0	**28·0**	*7·0*	15·2	86·2
Heath Pond	5·0	4·0	3·0	2·0	*2·0*	*2·0*	2·5	*2·0*	5·5	5·0	9·0	9·0	**11·5**	**11·5**	*2·0*	4·8	32·3
Wasing	5·0	6·5	**10·0**	5·0	*3·0*	3·0	4·5	5·0	4·0	5·0	9·0	9·0	9·0	**10·0**	*3·0*	6·0	27·0
Heath Lake	4·5	5·0	*3·0*	6·0	5·0	4·5	3·5	*3·0*	4·5	4·5	10·0	11·5	**14·0**	**14·0**	*3·0*	6·1	34·7
Bagshot	*8·5*	10·0	10·5	14·0	**28·0**	15·0	24·0	21·0	19·5	20·0	17·5	18·5	19·0	**28·0**	*8·5*	17·3	57·6
Aldermaston	6·5	7·0	5·5	7·0	7·0	6·0	8·5	7·5	5·5	*4·0*	5·0	9·5	**12·5**	**12·5**	*4·0*	7·0	19·6
Chapel Row	*23·5*	25·5	27·0	28·0	43·5	48·5	54·0	46·5	55·0	55·0	**57·0**	36·0	35·0	**57·0**	*23·5*	41·1	143·4
Round Pond	–	15·0	*11·5*	13·0	18·0	19·0	17·5	**18·5**	**24·5**	14·5	12·5	19·0	19·0	**24·5**	*11·5*	16·8	38·3
Kiln Pond	9·0	8·5	*8·0*	12·5	22·0	18·0	19·5	23·0	21·0	**24·0**	15·0	12·5	11·0	**24·0**	*8·0*	15·7	66·7
Egham	37·5	34·0	**42·5**	28·0	31·5	23·0	20·5	20·5	23·0	16·0	*14·5*	15·0	19·5	**42·5**	*14·5*	25·0	96·5
Leech	(171·0)	*7·0*	19·0	28·5	24·0	20·0	18·0	18·0	19·0	13·5	14·0	16·5	**44·0**	**44·0**	*7·0*	20·1	99·8
Farley	16·0	14·0	13·5	**25·5**	18·0	15·0	13·0	*12·0*	25·0	16·5	20·5	14·0	21·5	**25·5**	*12·0*	17·3	50·4
Whiteknights	11·5	10·0	10·0	*8·5*	9·5	9·0	9·5	10·5	6·5	12·5	**18·0**	11·5	12·0	**18·0**	*8·5*	10·7	24·1

pH water

	1954												1955		Max.	Min.	Mean	Sum of deviations
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.				
Three Firs	7·0	6·4	6·1	6·3	7·2	7·2	7·2	7·6	**7·7**	6·6	6·4	*5·9*	6·1	5·9	**7·7**	*5·9*	6·7	**7·5**
Hammond's	**5·5**	5·4	**7·4**	6·0	6·6	6·3	6·4	6·9	6·7	6·6	6·4	*5·2*	**7·4**	5·6	**7·4**	*5·2*	6·3	7·8
Eagle	6·9	6·7	**7·4**	6·8	7·0	6·8	6·3	6·6	6·5	6·7	7·1	6·4	6·8	*6·1*	**7·4**	*6·1*	6·7	**3·5**
Gormoor	**5·6**	**5·7**	*5·5*	5·7	5·9	5·8	**5·8**	6·4	6·4	6·0	**8·3**	*5·5*	6·2	5·8	**8·3**	*5·5*	6·0	6·0
Heath Pond	6·5	6·3	5·6	6·7	**5·3**	6·1	**5·8**	6·3	6·3	**5·5**	**7·1**	4·7	5·1	*4·1*	**7·1**	*4·1*	5·8	9·2
Wasing	6·8	6·3	*5·3*	5·9	6·2	6·9	6·3	7·2	**7·5**	6·2	6·4	6·0	6·6	5·7	**7·5**	*5·3*	6·4	**6·3**
Heath Lake	7·2	7·3	7·5	7·2	7·4	7·7	7·5	**8·0**	7·7	7·7	7·8	7·2	7·2	*6·4*	**8·0**	*6·4*	7·4	4·0
Bagshot	6·9	7·0	6·8	7·0	7·6	7·5	7·3	**7·7**	7·5	7·2	6·9	*6·6*	7·0	6·7	**7·7**	*6·6*	7·1	4·1
Aldermaston	7·5	7·5	7·2	7·4	7·6	7·5	7·4	8·0	**8·3**	7·6	7·5	7·2	8·0	*6·9*	**8·3**	*6·9*	**7·5**	3·4
Chapel Row	7·1	7·3	7·1	**8·3**	7·9	7·3	6·8	*6·6*	*6·6*	*6·6*	7·1	6·6	6·8	6·8	**8·3**	*6·6*	7·1	**5·1**
Round Pond	7·3	*5·9*	6·8	6·5	7·1	6·9	**7·8**	7·1	6·9	7·0	7·5	6·2	6·7	6·4	**7·8**	*5·9*	6·7	5·3
Kiln Pond	7·5	7·3	7·4	8·0	**8·2**	7·5	7·4	7·6	7·8	7·8	7·4	*7·2*	7·3	7·3	**8·2**	*7·2*	7·6	**3·5**
Egham	(**8·1**)	*5·5*	7·3	7·2	7·2	7·1	7·9	7·0	6·5	7·4	7·2	6·6	6·8	6·8	**8·1**	*5·5*	7·0	6·4
Leech	**8·0**	6·2	*5·9*	7·3	7·0	6·9	7·5	6·9	6·9	6·9	6·5	6·5	7·0	*5·9*	**8·0**	*5·9*	6·8	5·0
Farley	7·1	7·3	7·3	**8·1**	7·0	7·1	7·0	7·2	7·2	7·2	7·6	*6·8*	7·4	*6·8*	**8·1**	*6·8*	7·2	3·1
Whiteknights	7·6	7·5	*7·4*	**8·9**	7·5	7·8	7·8	7·7	7·7	7·8	7·6	7·6	7·6	7·7	**8·9**	*7·4*	7·7	2·6

pH sub-aquatic soil

Three Firs		6·3	5·5	*5·3*	5·8	6·1	6·5	**6·7**	6·5	5·8	5·8	5·6	5·8	5·9	**6·7**	*5·3*	6·0	4·6
Hammond's		5·6	**6·8**	5·9	6·2	6·0	5·6	5·4	5·8	5·7	*5·1*	5·2	6·0	5·3	**6·8**	*5·1*	5·7	4·5
Eagle		6·5	**6·9**	5·9	6·3	*5·8*	*5·8*	6·0	6·1	5·9	6·4	5·9	5·9	5·9	**6·9**	*5·8*	6·1	3·4
Gormoor		5·2	5·0	5·1	5·0	5·2	5·5	*4·9*	5·2	5·3	5·3	5·0	5·4	**5·6**	**5·6**	*4·9*	5·2	2·0
Heath Pond		5·4	**6·0**	5·0	4·8	5·3	5·0	5·1	5·6	4·9	5·5	4·9	4·9	*4·3*	**6·0**	*4·3*	5·1	4·2
Wasing		**7·2**	7·0	*5·2*	7·0	7·0	6·5	7·0	6·4	6·4	6·6	6·3	6·6	6·3	**7·2**	*5·2*	6·6	4·7
Heath Lake		6·5	**6·8**	6·6	6·2	6·7	6·7	6·4	6·5	6·4	6·4	6·2	*5·1*	5·5	**6·8**	*5·1*	6·3	4·5
Bagshot		6·3	6·3	6·4	6·4	**6·9**	6·7	*6·2*	6·8	6·4	6·5	*6·2*	6·3	6·4	**6·9**	*6·2*	6·4	2·0
Aldermaston		6·8	6·8	6·8	7·1	7·0	6·5	**7·2**	6·6	*6·0*	6·4	6·3	6·9	6·6	**7·2**	*6·0*	6·7	3·3
Chapel Row		6·5	6·3	**7·8**	6·4	6·3	*5·8*	6·0	6·1	6·0	6·5	6·3	6·5	6·3	**7·8**	*5·8*	6·4	3·8
Round Pond		*5·7*	6·7	6·3	6·1	6·4	**6·9**	6·2	6·7	6·4	6·3	6·1	6·3	6·3	**6·9**	*5·7*	6·3	2·7
Kiln Pond		*6·1*	6·5	7·0	**7·4**	6·7	7·0	6·4	6·5	6·5	6·6	6·5	6·9	6·8	**7·4**	*6·1*	6·7	3·4
Egham		*5·1*	6·7	6·8	**6·9**	6·4	6·8	6·7	5·6	6·8	6·5	6·2	6·4	6·6	**6·9**	*5·1*	6·5	5·8
Leech		5·4	*5·2*	6·8	**6·9**	**6·9**	6·2	6·7	6·4	**6·9**	6·8	6·8	6·3	5·8	**6·9**	*5·2*	6·4	6·1
Farley		*6·5*	6·8	**7·8**	6·6	6·9	*6·5*	6·5	6·9	6·8	6·8	6·6	6·9	6·6	**7·8**	*6·5*	6·8	2·8
Whiteknights		*6·0*	6·3	**8·1**	6·9	7·3	7·1	7·0	7·0	7·0	7·1	7·4	7·3	7·3	**8·1**	*6·0*	7·1	4·3

THE DETERMINATION OF NUMBERS OF LEATHERJACKETS IN SAMPLE TURVES

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(With 7 Figures in the Text)

Accurate determination of the numbers of leatherjackets (larvae of the *Tipula oleracea* group) in sample turves is necessary for economic as well as ecological purposes. Third and fourth instars and pupae can be fully recovered by examination of residues after the turf has been broken up, teazed out and washed carefully under a jet of water on a bank of sieves. For full recovery of first and second instars the washing must be followed by an adaptation of the flotation-separation technique (Salt & Hollick 1944). These 'mechanical' methods are, however, very laborious and time-consuming. Attention naturally turns, therefore, to the feasibility of making leatherjackets quit the turf of their own accord by 'repellant' methods (*cf.* MacFadyen 1955).

For larvae after the second instar, entomologists of the National Agricultural Advisory Service (N.A.A.S.) are actually using a repellant method, the 'St Ives Method' (Cohen 1953). Essentially this consists in bringing leatherjackets to the surface by pouring a solution of an irritant, St Ives fluid, on the turf in the field. The sampling unit is 1 sq. ft on which 1 pt of solution is sprinkled evenly. Practically nothing is known of the efficiency of this method. The efficiency could, of course, be established simply by washing the square-foot turves immediately after the St Ives treatment. Washing square-foot turves is, however, a formidable task, and a great deal of labour might be expended only to find that the St Ives method was after all unreliable for ecological purposes. We decided, therefore, to explore first the possibilities of an idea for another repellant method.

In 1939, one of us (A. M.) had tried to drive ticks, *Ixodes ricinus* L., out at the bottom of a layer of grass mat by heat advancing from an electric light bulb fixed just above the mat surface (the Tullgren funnel method). The results were not satisfactory. Rightly or wrongly he interpreted this as being a consequence of using a dry heat; the discomfort signalling retreat might be accompanied by decreasing capacity for locomotion because the tick loses water readily. The idea of trying a wet heat thereupon occurred to him. Ticks would not be desiccated and might well be driven up out of the mat by raising hot water slowly through it. As it happened, the idea was not tested then because the particular tick problem involved was solved in another way. But with the prospect of washing numerous square-foot turves, the idea seemed well worth trying on leatherjackets in 1954.

Leatherjackets live in tunnels which open on the soil surface. Preliminary trials

at raising hot water through turves did indeed result in leatherjackets (and many other animals) emerging on the surface with obvious haste. And so we proceeded to experiment with this method of extraction or, rather, expulsion, which we have called the *hot water process* (H.W.P.). Unknown to us until 1956, Nielsen (1953) had already devised a wet heat method for expelling enchytraeid worms from small cores of soil.

METHODS FOR THE HOT WATER PROCESS

(*a*) *The turves*

It was decided to examine turves of area 12 × 12 in. for two reasons: the standard turf size used by N.A.A.S. workers is the square foot, and at Cockle Park, Northumberland, where the work began in the 1954-55 season, the population was so low that there would have been too many blanks with a smaller unit size. When it was realized that the exceptional drought of late summer and early autumn 1955 had practically killed out the leatherjackets at Cockle Park, the main work was transferred to Spout Bank, Cumberland. Here, although much smaller sampling units were now possible because of high population density, the original unit size was retained, partly for purposes of comparison and partly to avoid modifications to the apparatus for the hot water process.

Turves were to be 3 in. deep, not including vegetation above the soil surface. This was decided from field knowledge of the maximum depth at which leatherjackets live.

Before cutting a turf, the grass was cropped to a height of about 1 in. An exact 12 × 12 in. square was then marked out by treading on an angle-iron frame. The vertical flange of this frame has a sharp edge and bites up to 1 in. deep in the soil. Exactness is necessary so that the turf will properly fit the apparatus for the hot water process. After marking, the turf was cut to a depth of 6-9 in. all round with a specially made, thin, flat, steel spade. If the turf is cut too shallow, it will break when being levered out. Once out, it was trimmed to 3½ or 4 in. depth and transported, grass uppermost, in a transparent plastic bag.

(*b*) *The hot water process*

At the laboratory, the turf was further trimmed neatly to 3 in. depth and the grass cut still closer, taking care, however, not to damage protruding larvae or pupae – if any.

Figure 1 shows the apparatus for the hot water process. Essentially it is two galvanized metal boxes, one within the other, the space between being a water-jacket. The inner box has a bottom of fine-meshed wire gauze through which water can pass. The turf fits the inner box tightly, its bottom resting on the gauze and its top 1½-2 in. below the rim. The process always starts with the water in the jacket ½ in. above the bottom of the gauze. The water is heated electrically and its temperature controlled at 90° C. If the water were allowed to boil, there would be difficulties with steam, and the base of the turf would tend to break up.

Water level in the jacket is raised by adding water, and, lagging behind, water level in the turf rises accordingly. In preliminary trials we started with the jacket water at tap temperature. When the jacket water reached 90° C, its level was raised half an inch every 10 min until flush with the soil surface. With this regime, heat rises slowly up through the turf (Fig. 2) and, for obvious reasons, rises faster at the edges than in the middle.

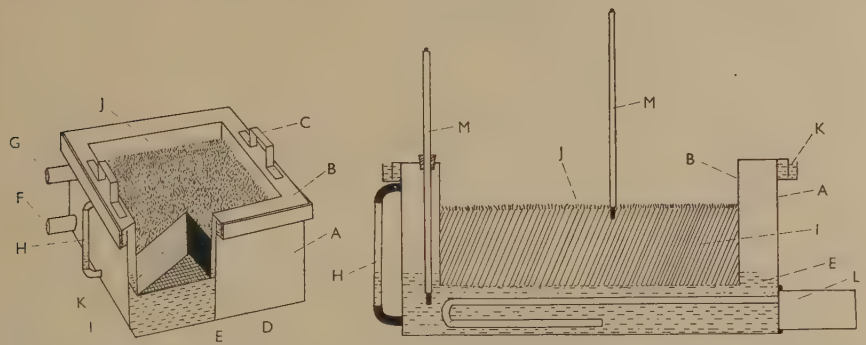

Fig. 1. Apparatus for the hot water process. A, outer galvanized metal box; B, inner galvanized metal box with C, handles for lifting and D, bottom of wire gauze; E, water (jacket); F, inlet pipe for water under mains pressure (also outlet for emptying the apparatus); G, overflow pipe; H, water-level gauge; I, turf in inner box showing J, close cropped grass; K, water-seal to prevent vapour escaping; L, electric heating element and thermostat; M, thermometers.

30° C appears to be the critical temperature for leatherjackets in the hot water process. This was clear from experiments using damp sand in a beaker with its base in water held at 90° C. Each leatherjacket (six separate trials) was placed at the bottom of a vertical tunnel in the sand, $\frac{1}{4}$ in. diameter and $1\frac{1}{2}$ in. deep. Appropriately placed thermometers showed that the leatherjackets started to move

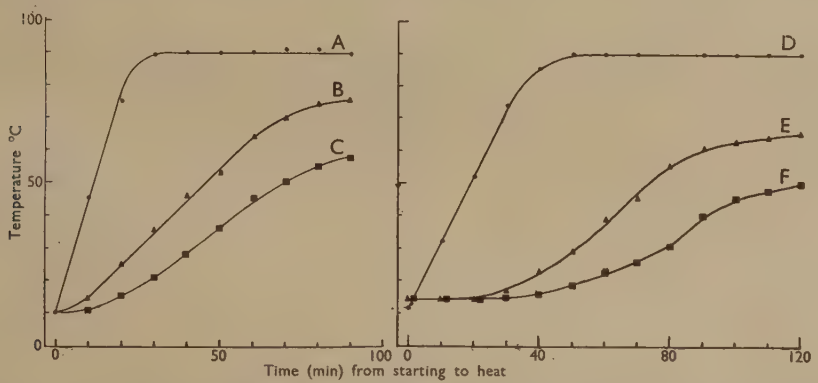

Fig. 2. The rise of heat through the turf. Temperatures: A, in the jacket; B, 2-2½ in. below the soil surface in the middle of the turf; C, 0-½ in. below the surface in the middle; D, in the jacket; E, 1 in. from the edge and 1½ in. below the soil surface; F, at the mid-point of the turf 1½ in. below the surface.

upwards when the temperature in their vicinity had risen to around 30° C. This finding suggested that, to be on the safe side, a turf should be heated until temperature at the surface mid-point is at least 40° C.

Controlled experiment showed that, except where there was much peat in the surface layers of the soil, the time taken for the temperature to reach 40° C just under the soil surface at the centre of the turf was practically the same whether the water was raised at 10 min intervals, at 3 min intervals, or not raised at all. There are physical reasons for this, of course, but it is enough here to note the fact merely as an important labour-saving finding.

The standard procedure finally evolved was this: A thermometer was placed with its bulb just under the soil surface at the mid-point of the turf. The level of water in the jacket stood at $\frac{1}{2}$ in. above the bottom of the turf until this thermometer registered 40° C. The water level was then raised all at once to a height which would (eventually) just flood the mat on the soil surface, and heating as well as observation was continued for a final 15 min. This flooding was a precaution against the insulating effect of the vegetation mat on the soil surface. In the mat, conditions only one-eighth of an inch above quite hot soil can be relatively cool. The odd leatherjacket, coming up early and therefore not excited by over-much heat, may lie still in the mat and so be overlooked until flooding forces it into view.

The time required for completion of the hot water process varies with the nature of the turf and other conditions, taking longer the heavier the soil, or the more peat in the surface layers, or the greater the soil-moisture content at lifting. Starting with the water in the jacket at 90° C shortens the time by 10-20 min. In that circumstance, the entire process may take 45-60 min with a lightish soil which is medium dry at time of lifting; on the other hand, it may take as much as 120-150 min with the heaviest peat-covered clay which is sodden.

As in the field, leatherjackets (or at least some of them) come out of their holes at night to wander on the surface of a turf kept in an unlit laboratory. Some fall down the sheer sides of the turf and so cannot regain their holes on the surface. Most of these are found at the bottom of the bag in the morning. But, as we became aware early on, the occasional individual may find some cleft or cranny at the turf base into which it bores out of sight before light. Such an individual has, of course, no egress to the surface; it can not, therefore, retreat from uprising heat and so is killed and retained in the turf during the hot water process. This can be avoided by storing turves under a bright light overnight, or, as in the present series of experiments, by processing turves on the same day as they are taken from the field.

During the hot water process the surface of the turf must be watched all the time and leatherjackets must be picked off as soon as they have emerged fully. When light shining on the turf is too bright, leatherjackets will partly emerge and then retract for a while. This reaction does not occur to any great extent with a 4-ft, 40-watt, 'natural' fluorescent tube light suspended 3 ft above the turf. It is usually better not to attempt picking off a leatherjacket with forceps until it is right out, otherwise the touching will cause it to retreat and so increase the labour of observation. Under the light prescribed above, leatherjacket larvae usually emerge

hastily, lash and twirl for a little, and so are easily noticed. This is particularly the case where the grass and mat are not very dense and can be cropped short enough before heating. Otherwise, their arrival may be noted by upward surges in the mat caused by 'back-arching'; if this is missed, the individual will be seen later when it comes right out on the surface at flooding. As would be expected (*see* before), those individuals living nearest to the edges of the turf emerge first, and larvae emerge as a rule when the temperature near the soil surface is around 40° C. Thus in each of twelve turves where an individual came up within a radius of 2 in. round a centrally placed thermometer, this occurred when the temperature averaged 39° C (36-42° C).

Pupae also respond to the hot water process. Because of their colour they are hard to see unless they move and even then may be missed if the grass is too long. At best they come only half out, flicking the anterior half of the body from side to side while the posterior half remains in the hole. Unfortunately the flicking soon becomes intermittent. But pupae are not missed provided the grass is cut short and a close and continuous watch is kept throughout heating and flooding.

Of the other species brought up by the hot water process, only earthworms are a nuisance. They distract the eye with their writhings, and when numerous may even hide leatherjackets beneath them. Earthworms should be picked off as soon as they surface.

(*c*) *Checking by turf-washing*

To find whether any leatherjackets failed to respond to the hot water process, each turf was broken down on a bank of large graduated sieves as soon as it cooled sufficiently for handling. But first it had to be ascertained how 'cooked' leatherjackets would stand up to this turf-washing. On the average, leatherjackets remaining in the turves would suffer 90 min at 90° C. Twenty individuals collected in the field (April) were brought to 90° C in a beaker of water and held at that temperature for 90 min. At the end of this cooking, the leatherjackets were all intact with body-axis perfectly straight, had not changed colour significantly (if anything, only very slightly less dark), and felt quite tough when pinched or pulled with the fingers. Some of them were now inserted in turf debris on a sieve and subjected to the severest possible jet-pressure (very much severer than normally used). They could not be trapped under the jet even when it was vertical; they just rolled away like elongated barrels, quite unharmed. When deliberately immobilized on the sieve they were soon reduced to an empty skin (which would be difficult to see) but so also were live larvae though it took 1½ to 2 times as much jetting. However, normal jetting is much less fierce and not vertical but at a low angle to the sieve. Thus cooked larvae should have no chance of being pinned against the sieve and should be seen as they roll away among the debris. We tested this impression with the remainder of the cooked larvae, as follows. Two turves, A and B, were cut. In turf A, four cooked larvae were inserted, the first in the mat, the second at ½ in. depth in the soil, the third at 1 in. depth and the fourth at 2 in. depth. To position the latter three, a cork-borer was used, the vertical tunnels

being packed with soil after insertion of the larvae. In turf B, three cooked larvae were inserted in the same manner, one in the mat, one just under the soil surface, and one at 1½ in. depth in the soil. The turf-washer (R. E. C.) had no inkling of what had been done to these turves, yet he recovered all seven cooked larvae intact. We concluded that turf-washing, provided it was done on the same day, would yield all leatherjackets killed by the hot water process. In any turf there might also be cooked leatherjackets which were not killed by the hot water process but which had died previously in the field. This is dealt with below.

RESULTS FROM THE HOT WATER PROCESS

The bulk of the turves studied came from a section of Davey Houses Field, Cockle Park, Northumberland, in 1955 and from Rushy Field, Spout Bank, Cumberland, in 1956. Both fields have a light-medium soil. For comparison, some heavy soil (clay) turves were taken from North Field, Paradise, Cockle Park. There was no difference in the efficiency of the hot water process in lighter and heavier soils. A summary of the results is given in Table 1.

Owing to the impossibility (so far) of separating their larvae, three Tipulids, *Tipula paludosa* Meig., *T. oleracea* L. and *T. czizeki* de Jong, have come to be known as the '*Tipula oleracea* group'. During the flight seasons of 1955 and 1956, large samples were taken of adults belonging to this group which were working over the study fields. *T. czizeki* was never found but there was a small proportion of *T. oleracea* among the *T. paludosa*. Surprisingly, only *T. paludosa* adults have emerged from samples of larval and pupal leatherjackets of the *T. oleracea* group taken from these fields at intervals through both years and reared in the laboratory. However, on rearing leatherjacket samples from forty-seven golf courses distributed over the British Isles, Lovibond (1937b) found that forty-five of the forty-seven samples yielded *T. paludosa* and only four yielded *T. oleracea*. Thus it may be assumed that the results in Table 1 are predominantly if not wholly for *T. paludosa*. The point may yet be settled because we have preserved a large series of larval samples against the possibility of being able to distinguish later between *T. paludosa* and *T. oleracea*.

(*a*) *Leatherjackets remaining in the turf after the hot water process*

Dead leatherjackets found in turf-washing were immediately examined externally and dissected in order to decide which had been killed by the hot water process and which had died in the field before the turf was cut. In Table 1 these leatherjackets are classified according to their post-mortem appearance.

'Dead before H.W.P.', includes larvae and pupae whose tissues were in an advanced state of decomposition. Some contained parasites, some were diseased, but all showed disintegrating tissues, making it certain that they were dead before the turves were cut.

'Probably dead before H.W.P.', includes larvae showing some of the first signs of decomposition: fat body fragile, muscles beginning to come away from their

Table 1. *Results from treating square-foot turves with the hot water process, April 1955 to August 1956*

Up to the end of November 1955 all turves were from Davey Houses Field, Cockle Park, Northumberland, except 6 turves in April, 4 in May, 2 in October and 4 in November which came from North Field, Paradise, Cockle Park; after November 1955 all turves came from Rushy Field, Spout Bank, Cumberland.

	Number of turves	Individuals recovered alive from H.W.P.		Individuals recovered dead from washing after H.W.P.								
				Dead before H.W.P.		Probably dead before H.W.P.		Probably killed by H.W.P.				
								Crushed or cut at lifting of turf in field		Larvae about to pupate	Cause uncertain	
		Larvae	Pupae	Larvae	Pupae	Larvae	Pupae	Larvae	Pupae		Larvae	Pupae
April	16	39		1	–	–	–			–	–	
May	22	63	–	4	–	–	–	½	–	–	–	–
1-28 June	20	42	–	11				–	–	–	–	–
29 June-7 July	12	19	1	8	–	–		–	–	3	–	–
12-18 July	12	13	4	3	1		–	–	2	–		–
25 July-3 August	8	9	7	2	–		–	–	–	1	–	–
18 October	2	10	–					–	–	–	–	
November	8	13				–	–	–	–	–	–	
December	5	301	–	1	–	–			–	–	–	
January	6	289	–	1	–	–	–		–	–	–	–
March	8	317	–	9	–	–	–	–	–		–	–
April	8	274	–	22	–	–	–	½	–	–	–	
1-19 May	4	124	–	3	–				–	–	–	–
28 May and 8 June	8	156		11	–	2		–	–	1	2	–
22 June and 6 July	8	112	2	19	1	1	–	–	–	1	–	–
20 July and 3 August	8	45	30	11	5	–		3	–	4	1	2
10 and 16 August	8	4	9		2	–	–	–	1	–	–	1
Totals	163	1830	53	106	9	3	–	4	3	10	3	3

attachments and turning brown at the tips, body fluid slightly cloudy. Early tests showed that larvae may show the first signs of decomposition within 24 h of death; hence the need for examination immediately after turf-washing. Only three larvae came into this class.

The remaining class, 'probably killed by H.W.P.', is divided into three sub-classes: (i) 'Crushed or cut at lifting of turf in field': these larvae showed fresh wounds undoubtedly caused by the marking square or the cutting spade. The wounds, more or less severe, would interfere with locomotion which would also be hindered if not prevented altogether by the partial destruction of the tunnels inevitably accompanying the infliction of wounds. (ii) 'Larvae about to pupate': the form is shorter and thicker than the normal larval corpse. On dissection the fat body appears dense and amorphous, closely investing the internal organs; it breaks away readily in irregular lumps. Usually the body wall muscles are detached from the cuticle and sunk into the cylinder of fat body. Occasionally the cuticle of the pupa is present. All larvae recorded in this sub-class were probably incapable of locomotion (the muscles being more or less detached) and so were unable to escape from the hot water. All had healthy tissues. Experience with *Tipula paludosa* in culture has shown that, at 20° C, the immobile stage lasts less than 5 days. (iii) 'Cause uncertain': these larvae and pupae appeared perfectly healthy inside and out. Possibly they were living near the turf edges and their tunnels were blocked above them by the marking square or the cutting spade. Rather limited observation, yet to be confirmed, suggests that the larva descends to a depth of 2 or 3 in. to pupate, and the pupa later ascends probably by stages until it finally comes to rest partly protruding from the soil. Since prepupation had already started in the population the larvae as well as the pupae in question could have been deep enough to suffer squashing of the upper regions of their tunnels without injury to themselves. Moreover, in the case of the pupae, tunnel blockage might not even be necessary. A pupa 2 or 3 in. down, being less efficient at locomotion than a larva, might be unable to ascend faster than the paralysing heat rises.

Omitting the two half-individuals, both tail-ends (the convention in quantitive work is to count head-ends only), 140 leatherjackets were got from washing 163 square-foot turves which had previously yielded 1883 live individuals by the hot water process. Of these 140, 115 or 82% were certainly dead before the hot water process and therefore do not enter into the question of the process's efficiency.

(*b*) *Efficiency of the hot water process*

The percentage of the total live leatherjackets recovered by the process is an expression of its efficiency, and is shown in Fig. 3. The calculation includes all leatherjackets other than those known to be dead before the start of the process. From mid-October until the first prepupae occur, usually in June, the process has an efficiency of 100%. This covers the third and final larval instars at least. After prepupation starts in the population and until adult emergence is complete, usually September, the efficiency is less than 100%. In 1955 it ranged from

87-94%, mean on totals of individuals (53/59) 90%, and in 1956 from 87-98%, mean (358/377) 95%. The second year probably gives the truer picture because the numbers of individuals in the samples were very much larger. These percentages are based on groups of eight or twelve turves (see Table 1). Actually, the efficiency was 100% in four out of every five turves from 29 June to 3 August 1955 and in two out of every three turves from 28 May to 16 August 1956.

(*c*) *Discussion*

Judging by the fact that enchytraeid worms respond to the process, it is likely that first and second instars of the leatherjacket would do likewise. There may be difficulty, however, in seeing them all in the tangle of grass and mat however short, in which case the recovery would not be complete. We intend to look into this. Alternatively, Nielsen's method (1953) may prove suitable.

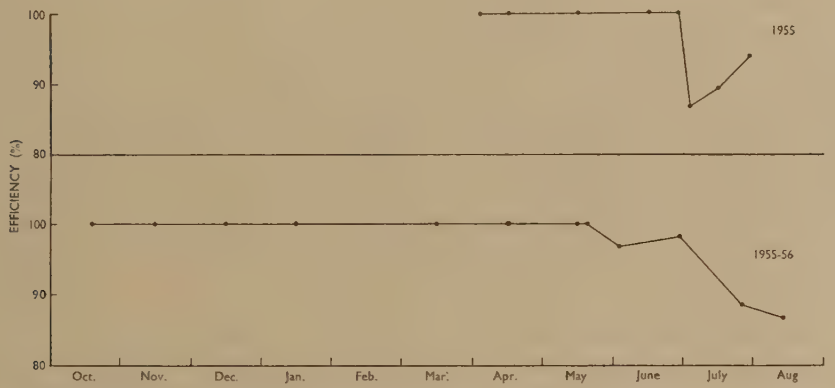

Fig. 3. The efficiency of the hot water process expressed as a percentage of the total live leatherjackets present. See text and Table 1.

Although efficiency drops below 100% after prepupation sets in, the majority of prepupae and pupae do respond to the process. This might be expected since the helpless stage with muscles detached is short, and only a fraction of individuals will be in it at any one time. Moreover the efficiency here may well be underestimated. For one thing, individuals recorded in Table 1 as probably dead may in fact have been dead before heating started; for another, the victims of wounding and tunnel-blocking can hardly be expected to respond to the process. It seems likely that if wounding and tunnel-blocking could be avoided, all healthy individuals except those on the point of pupating would be recovered. In that case, the mean efficiency after prepupation set in should have been 98% in 1956.

Wounding and tunnel-blocking could probably be largely avoided by lifting a 14 × 14 in. turf and sawing off a 2-in. strip all round. Sawing will not give rise to the pressures which result from forcing tools down into the turf and from levering the turf out and breaking it free from its base with the spade.

CHECKING THE ST IVES METHOD BY FOLLOWING IT WITH THE HOT WATER PROCESS

The efficiency of the St Ives method can be checked accurately by subsequent turf-washing, but the labour is much less if the hot water process is substituted. This we did, but before dealing with the results it is necessary to describe and discuss the St Ives method in some detail.

(*a*) *History and practice of the St Ives method*

This method was apparently invented by T. W. Evans at the St Ives (Greenkeeping) Research Station, Yorkshire (Dawson 1932, pp. 189-90). Dawson tells us that the stock solution of the 'expellant' was an emulsion comprised of 16 parts (by volume) of orthodichlorobenzene, 4 parts of a 10% solution of sodium oleate in water, and $\frac{1}{8}$ parts of Jeyes' Fluid. The stock solution is now sold under the misnomer (see later): 'Jeyes' Leatherjacket Exterminator'. The working solution, which we shall call 'normal' St Ives fluid, was 1 part of stock solution mixed with 400 parts of water, and was applied at the rate of 1 gal per sq. yd of turf. This 'dilution was arrived at on the basis of trials on the effect of the emulsion on the grass itself. In other words we had to arrive at a dilution which would bring up a big proportion of the grubs without material damage to the grass. It was, of course, specifically designed for use on turf [golf, bowling, tennis and cricket greens, and lawns, etc.] and not for any other purpose' (R. B. Dawson, private communication). Advisory entomologists still use the same working solution at practically the same rate, 1 pint per sq. ft (Cohen 1953).

St Ives fluid irritates leatherjackets so that they emerge on the surface, obviously in an attempt to escape the irritation. Both Dawson (1932) and Barnes (1941) hold that, as used, the fluid itself does not kill. Barnes says: 'The leatherjackets come to the surface within a few minutes and are in no way permanently damaged. If not removed, they will later descend once more into the turf and soil.' We confirmed these observations. In addition, we found that leatherjackets, expelled by St Ives treatment in the field or recovered by H.W.P. after St Ives treatment, will survive in laboratory culture to emerge as adults. As used in the field, the fluid is certainly not an 'exterminator' nor does it seem to do more than irritate at the time. The St Ives workers did not say that it was an exterminator; they merely recommended it as a means of expelling leatherjackets on the surface so that they could be swept up and destroyed.

On the question of when, after applying the fluid, to begin counting leatherjackets, Barnes (1937) states: 'The appropriate solution [St Ives fluid] is applied with a watering can with rose to the turf and in a few minutes the leatherjackets come to the surface. If they are not collected within about 10 min, they burrow back into the soil.' Dawson & Ferro (1936) say: 'Time allowed before counting larvae after application of the ... emulsion ... [depends] ... upon the prevailing weather conditions.' Escritt (1947) adds: 'It has been found impracticable to use a specified time interval [before counting] since weather conditions influence the

depth and mobility of the grubs.' Incidentally, in the literature we can find no substantial facts concerning the levels at which leatherjackets live throughout the year, nor about weather-influence on levels.

Apparently these earlier workers waited a certain unspecified number of minutes after applying the St Ives fluid and then counted the leatherjackets. Cohen (1953), in his report of a survey of leatherjacket populations by the National Agricultural Advisory Service (N.A.A.S.), is a little more helpful for he says: 'The leatherjackets visible on the surface within five minutes of treatment were to be counted.' So far as we can gather, this really meant making a count at the end of the five minutes. Recently a N.A.A.S. entomologist, who had worked with Cohen, kindly gave us a demonstration of his own practice. To what extent this is standard practice in the Service we do not know, but the procedure was as follows. He cut the grass close with shears, marked out the square foot by pressing on a sharp-edged metal frame, applied one pint of fluid with an ordinary watering can, stuck a wire marker in the centre of the square foot, then carried all the gear to the next square foot twenty paces away. After dealing rapidly in this way with five separate square feet, he left his gear and returned to count the leatherjackets on the first square foot treated, then the second, and so on up to the fifth, collecting the five markers as he went along. He then repeated this 5-fold procedure another three times until he had done twenty square feet. Timing showed that counting started in each square foot at the fifth or sixth minute after application of the fluid, and lasted from 30 sec (low leatherjacket densities) to 90 sec (high densities). Twenty square feet were completed in under one hour.

Barnes (1941) holds that counts by the St Ives method remained fairly steady at Rothamsted from November 'till the spring'. The data for November to January seem to have been provided by 'Miss Lovibond, (1937a)', but these data were not published by her then nor, so far as we can discover, later. However, Barnes maintains that up to spring 'the standard of efficacy of the [St Ives] sampling is that not less than 80 % of the leatherjackets are brought to the surface and found'. He gives no data and does not specify the method whereby he came to this conclusion. There is no mention of digging up turves to find how many leatherjackets were left behind by the treatment. In short, there is no means of judging his claim that the St Ives method is not less than 80 % efficient up to spring. In the same paper, Barnes showed clearly that counts by the St Ives method dropped more or less steadily after March or April to zero in June or July. The control data for experiments by Escritt (1947) confirm this at Aberdeen. Barnes attributes the fall-off in counts mainly if not wholly to increasing failure of St Ives fluid to bring up all leatherjackets after March or April. As it happens Barnes was partly correct in this interpretation (see later) but he had no strict proof. For this he should have investigated turves at intervals. In fact he did so only once (28 May 1940), finding ten leatherjackets (presumably by hand sorting) on digging up a square yard which had just yielded four by the St Ives method.

Barnes suggests several reasons for the increasing failure of the St Ives method as winter gives way to spring and summer, but the important point is that he gave

no dependable indication of the efficiency of the method at its best from November to March.

(*b*) *New facts important in field practice of the St Ives method*

The St Ives method, using 1 pint normal fluid to 1 sq. ft of turf, has been investigated in every month, except August and September, from November 1954 to July 1956, on fourteen pastures with soil ranging from light-medium to heavy. The method was standardized thus: The grass was always cut as close as possible in order to lessen the chance of overlooking a leatherjacket. A 12 × 12 in. metal frame 5 in. high was pressed 1-1½ in. into the ground by standing on an outer flange; this prevented fluid from running out over the edges of the square foot. Exactly 1 pint was evenly distributed over the square foot from a special can which delivered fluid through a line of equally spaced small holes in a straight

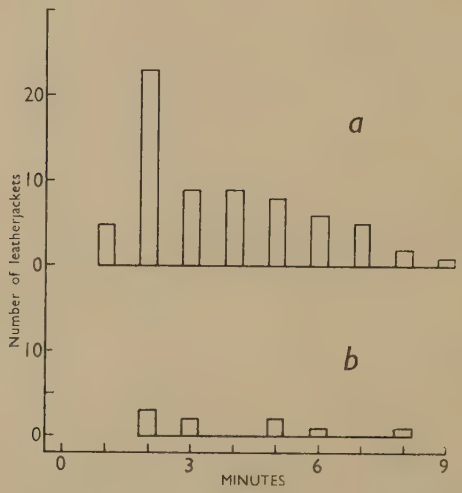

Fig. 4. Arrival times for all leatherjackets surfacing after application of St Ives fluid to two areas of turf, each 1 sq. ft. Cow pasture, Spout Bank, Cumberland, 15 December 1955; soil temperature 42° F. (5·5° C.). *a*, dense population – 68 individuals came up; *b*, relatively thin population – 9 individuals.

brass strip 12 in. long. By holding the face of this strip squarely within the metal frame and moving it backwards and forwards the full 12 in. steadily and according to the rate of delivery, a reasonably even coverage was achieved. One pint was delivered in about 15 sec. In every square foot tested, the interval between application of the last drops of fluid and the arrival on the surface of each individual leatherjacket was recorded to the nearest minute; this interval will be called the 'arrival time'. Thus an arrival time of 2 min means that the individual arrived on the surface between 1 min 30 sec and 2 min 30 sec after the fluid had been applied. As typical, Fig. 4 shows the distribution of arrival times for individuals

surfacing in a densely populated square foot and in a relatively thinly populated square foot treated in one field in December when soil temperature was 42° F (5·5° C).

The arrival time of any leatherjacket on the surface would be expected to be influenced by a number of factors, such as: (1) the depth at which it lies; (2) the time taken for the right amount of irritant to reach it, which will be governed by physical character of turf, and by moisture content, etc.; (3) the rate at which it travels upward, which will be related to its physiological or developmental state and soil temperature, etc. By our wide choice of pasture type and range in dates of observation, the gamut of conditions must have been fairly well covered: mat, dense to thin; soil, heavy to light; soil moisture, sodden to practically dry; soil temperature, at about 1 in. depth, 33-61° F (0·5-16·1° C; the fluid is not, of course, used on frozen ground); time of year, October to July. Leatherjacket arrival times actually differed little under all these conditions. By far the greatest differences (and they are relatively small) were observed not in relation to mat character, soil type, or moisture content, but in relation to soil temperature. This varies with the weather but is mainly governed by season, which brings in differences in physiological or developmental state and in habits of leatherjackets in the larval and possibly prepupal stages (the St Ives method never yields pupae in field practice). Therefore, for deciding when to begin and end counting after applying St Ives fluid, classification of arrival times according to soil temperature alone will give the maximum useful information. The soil temperature range has been divided into low, medium and high classes, respectively: 33-39° F (0·5-3·9° C), occurring November to February; 40-49° F (4·4-9·4° C), October to January and March to May; and 50-61° F (10·0-16·1° C), March to July.

Fig. 5*a-c* shows the arrival time of the first leatherjacket to appear after treatment. At low soil temperatures, the first to arrive appeared in anything from 1 to 8 min (mean 3·3 min); at medium, 1 to 8 (2·7) min; and at high, 0 to 5 (1·7) min. The difference between low and medium temperature results should probably be greater (and this applies also to Fig. 5*d-f*) because forty-eight of the fifty-eight square feet classed as low had temperatures of 38 or 39° F, *i.e.* not very different from medium temperatures. Fig. 5*d-f* shows the arrival times of all leatherjackets up to the tenth minute. Whatever the temperature, leatherjackets arrived as late as 10 min after applying the fluid, but the mean arrival time was less the higher the temperature, viz. low, 5·0 min; medium, 3·8 min; high, 2·1 min. Actually, observation was quite often extended to the fifteenth and sometimes to the twentieth minute, but when nothing came up after the tenth minute this fact was seldom recorded. At high temperatures, no leatherjacket ever came up after the tenth minute, as would be expected from Fig. 5*d-f*. In our notes, the results of extended observation have been recorded for twenty square feet at medium temperatures. These yielded a total of 228 individuals but only one (0·4%) came up after the tenth minute (actually at the eleventh minute) and the temperature, 42° F (5·5° C), was near the lowest in the medium range. Similarly we have records for seventeen square feet at low temperatures. These yielded 336 individuals, of

which 7 (2·1 %) came up in the eleventh minute, 9 (2·6 %) in the twelfth minute and one (0·3 %) in the thirteenth minute. All those coming up after the tenth minute were from four square feet at 33° F (0·5° C), while the other thirteen square feet had temperatures of 37-39° F (2·2-3·9° C). Thus, it is safe to say that practically no leatherjackets will come up later than the tenth minute except when the soil surface is within a degree or two of freezing. If the grass is not cut close enough,

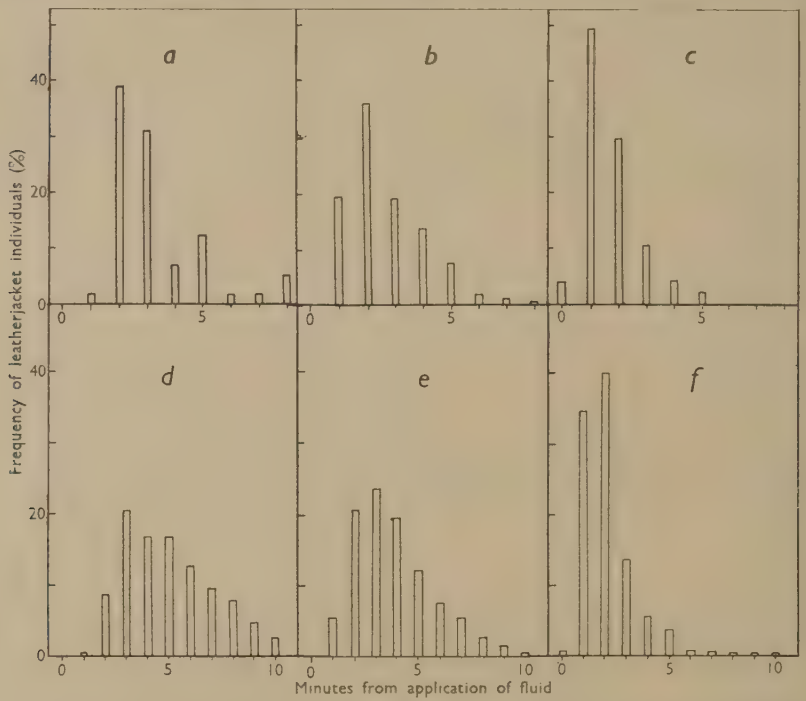

Fig. 5. Frequency of arrival times of leatherjackets in each minute from the application of St Ives fluid (at 0 min). *a*, *b*, *c*, arrival of the first individual in each of (*a*) 58 sq. ft areas at low, (*b*) 173 areas at medium, and (*c*) 97 areas at high soil temperatures. Frequencies are shown as percentages of 58, 173 and 97 respectively. *d*, *e*, *f*, arrival of all individuals up to the tenth minute in each of (*d*) 59 areas (433 leatherjackets) at low, (*e*) 177 areas (1229 leatherjackets) at medium, (*f*) 101 areas (812 leatherjackets) at high soil temperatures. Frequencies are shown as percentages of 433, 1229 and 812 respectively. For the actual soil temperature ranges see text.

odd leatherjackets may seem to come up later at medium temperatures, but this is due to their primary arrival on the soil surface being hidden from the observer by herbage and mat.

Clearly if counting is confined to the fifth or sixth minute after applying the fluid, the numbers got will be considerably less than the total actually brought up. On our data, the loss at low temperatures can be 25-37 %; at medium temperatures, 11-18 %; and at high, 1-2 %. Now sampling by the St Ives method is normally carried out from October to May, *i.e.* at low and medium soil temperatures only,

so the underestimate of numbers responding to the fluid can be quite serious—anything from 11 to 37%. Moreover, in this calculation it is assumed that before the fifth or sixth minute no leatherjackets have wandered off the square foot or come into it, for the soil 2-3 in. around the outside is also affected to a lesser extent; it is also assumed that none have disappeared back into the mat or soil.

If the frame is taken away after applying the fluid, some leatherjackets do wander off the square foot when left to their own devices, since they are very active for the first minute or so; our impression was that considerably more went off than came on. The question of disappearance back into the mat or soil was investigated every now and then by leaving a leatherjacket to see what it did, instead of picking it off as soon as it appeared. Each of these leatherjackets was observed continuously for 15 min (some for 20 min). Altogether twenty-nine individuals were so observed and results were as follows: After lashing about on the surface, fifteen leatherjackets disappeared entirely from view in 2, 2, 2, 2½*, 3, 3½†, 4½‡, 4½, 5, 5½, 6, 7, 7, 7½ and 11 minutes. Except for the individual marked*, which reappeared 2 min later and remained in full view all the time, none came up again. Search, at the end of the observation period, revealed the fourteen well down in the mat or making their way into the soil, but they were very difficult to find even though their points of disappearance were marked by wire pins. Four leatherjackets were considerably more than half hidden among the grass and mat in 2, 3, 5 and 8½ minutes. They remained thus motionless until the end of the period. If one looked away for a moment it was exceedingly difficult to spot a partly hidden individual again. Individuals in the first group are in this partly hidden state, sometimes for a minute or two before they finally disappear; for example, the individuals marked† and ‡ were about two-thirds hidden 1 min and 3 min respectively before they finally disappeared. The remaining ten leatherjackets were in full view on the surface throughout the observation period. After the first violent agitation, they moved less and less, with periods of inaction increasing in duration.

If the arrival time for leatherjackets in the first group were 1 min, then a count starting in the fifth or sixth minute would miss 5 or 8 individuals respectively; with arrival time 2 min, the loss would be 3 or 5 individuals; with arrival time 3 min, 0 or 3; and with arrival time 4 min, 0 and 0. Moreover, it is likely that leatherjackets in the second group would not all be seen, and some in the first would have actually 'disappeared' to all intents and purposes earlier, because partly hidden individuals are not easy to see even with careful searching. Counts starting later than the sixth minute would involve still larger errors. However, leatherjackets do not all come up in any one particular minute. Since their arrivals are spread over 10 min we have probably exaggerated the possible error arising from individuals disappearing partly or wholly before the count begins. Yet, whether large or small, the possibility of error is undoubtedly there, and will increase the later the count begins.

To sum up: on application of St Ives fluid, individual leatherjackets will surface at any time during the ensuing 10 min (13 min if the surface soil is near freezing); if left alone, some re-enter the turf and disappear in 2 or more min; others remain

on the surface for any length of time up to at least 20 min. Clearly, then, the total of those responding to St Ives fluid can be got only in the following way: the grass must be cut as closely as possible. After applying the fluid, the operator must observe the turf surface continuously for the following 10 min (15 if the soil temperature is near freezing point), and pick off (count) each leatherjacket immediately it arrives. This means that an operator can only treat one square foot at a time and needs from a little less than 4 to a little more than 5 h to do 20 square feet. For strictly comparable results, the frame (sunk 1 in.) and special 'watering can' are required.

(*c*) *Efficiency of the St Ives method*

As noted earlier, the efficiency of the St Ives method was checked by following it up with the hot water process. This appeared justifiable on the grounds that

Fig. 6. Efficiency of the St Ives method at Rushy Field, Spout Bank, Cumberland, expressed as a percentage of the total live leatherjackets in the turf. See text and Table 2.

field treatment with St Ives fluid does no real harm to leatherjackets, but to make sure, groups of four turves were washed after H.W.P. on three occasions. There was no evidence that previous St Ives treatment had incapacitated any leatherjacket so far as response to H.W.P. was concerned. A note of caution must be added in regard to following St Ives treatment with the hot water process. During H.W.P., turves previously treated with St Ives fluid give off poisonous fumes, which must be sucked away from the observer by a fan behind the apparatus.

Preliminary efficiency tests were made in 1955 at Davey Houses and Prestwick Whins, Northumberland. Both places have a light-medium soil. In June at Davey Houses, twelve square-foot turves yielded a total of two leatherjackets from St Ives treatment in the field, and twenty-eight from the hot water process afterwards in the laboratory, indicating an efficiency of only 6·7% for the St Ives

method. Similarly, in November at Prestwick Whins, the total numbers for four turves were ten and three leatherjackets respectively, an efficiency of 76·9%. Similar results were got from two fields with heavy soils. Physical character of turf seems to play little or no part in influencing efficiency so long as the herbage is cut close before application of the fluid. Fig. 6 shows the efficiency of the St Ives method from November 1955 to July 1956 at Spout Bank, Cumberland (light-medium soil). This was calculated from the data in Table 2, allowances being made

Table 2. *Results from treating square-foot turves first with normal St Ives fluid and then with the hot water process. Spout Bank, November 1955 to July 1956*

	Number of turves	Individuals recovered from St Ives treatment		Individuals recovered from subsequent H.W.P.	
		Larvae	Pupae	Larvae	Pupae
November	4	211	–	39	–
December	2	68	–	6	–
January	4	137	–	39	–
February	4	151	–	18	–
March	3	89	–	13	–
April	2	64	–	3	–
May	2	49	–	12	–
June	3	20	–	27	–
July	2	1	–	14	3

for the slight inefficiency of the hot water process itself in May, June and July. From November to May, efficiency varied between 78% and 95%, but in June it dropped to 42% while in July it was only 5%. It should be noted, also, that the St Ives method does not bring pupae into view in the field (see Table 2). Although the

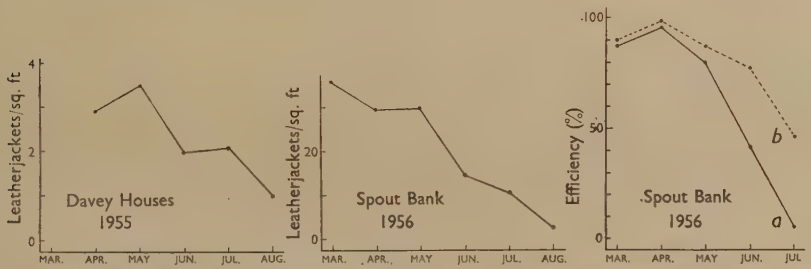

Fig. 7. Leatherjacket density and the efficiency of the St Ives method through spring and summer. *a*, part of Fig. 6; *b*, calculated from Table 3 omitting the data in column (A).

numbers of turves used in these efficiency tests were relatively small, the numbers of leatherjackets involved each month were quite large. It seems safe, therefore, to conclude that up to May the efficiency of the St Ives method was relatively stable, the mean being 85·5% for the twenty-one turves concerned, but thereafter it dropped rather steeply.

Fig. 7 indicates that Barnes was mistaken in thinking that the fall in his St Ives

counts from March onwards was due almost wholly to decreasing response to the fluid. The fall in numbers of leatherjackets actually inhabiting the turf is as steep as, and probably starts earlier than, the fall in response.

(d) Effect of increasing the strength and volume of St Ives fluid

A little work was also done at Spout Bank on the effect of doubling the strength and the volume of St Ives fluid. Table 3 shows the percentages of leatherjackets

Table 3. *Results from using normal and double strength St Ives fluid at the rate of 1 and 2 pints per square-foot*

One square foot was given each treatment on each date. The number of individuals which did not come up in response to the fluid, is expressed as a percentage of the total individuals in the turf (shown in parenthesis beside each percentage).

	Normal Strength		Double Strength	
1956	(A) 1 pint	(B) 2 pints	(C) 1 pint	(D) 2 pints
1 March	25·9 (27)	7·1 (28)	16·7 (18)	10·5 (19)
8 March	6·9 (29)	20·9 (43)	13·6 (44)	12·8 (39)
23 March	8·7 (46)	8·3 (36)	0·0 (37)	0·0 (29)
6 April	6·9 (29)	0·0 (22)	7·1 (14)	0·0 (12)
20 April	2·6 (38)	0·0 (38)	5·9 (17)	0·0 (29)
4 May	20·0 (30)	5·4 (37)	0·0 (33)	3·3 (30)
18 May	19·4 (31)	35·1 (37)	0·0 (23)	24·1 (29)
1 June	55·0 (20)	19·0 (21)	29·2 (24)	5·0 (20)
14 June	63·6 (22)	50·0 (8)	25·0 (12)	0·0 (8)
29 June	40·0 (5)	33·3 (9)	25·0 (4)	18·8 (16)
12 July	100·0 (13)	63·6 (11)	75·0 (8)	0·0 (9)
27 July	80·0 (5)	50·2 (2)	33·3 (3)	100·0 (2)
On Totals	24·4 (295)	16·4 (292)	12·2 (237)	8·7 (242)

which failed to come up with the various St Ives treatments. Incidentally, double strength St Ives fluid does not seem to injure pasture grass. Before applying these St Ives treatments, samples of soil on the outside edge of each square foot were taken for estimation of moisture content. From March to July, moisture content decreased irregularly from about 35-40 % down to 25-30 %. Differences between the four turves on any one day were negligible, ranging from 1 %-4 % with one case of 9 %. The data need not be given in detail since no consistent correlations, between results from different treatments and soil moisture content, could be found. In general practice we found that the fluid took a little longer to sink into the ground when the soil was very wet or very dry with a baked crust on the surface, but soil moisture conditions seem to have little or no effect on the results of St Ives treatment in the field.

The last row of Table 3 (percentages 'On totals') would seem to suggest that efficiency is increased by doubling the volume or the strength of St Ives fluid. There were twelve trials altogether. Two pints gave a better result than one pint in ten trials of normal strength (N.S.) and in eight trials of double strength (D.S.). Similarly, D.S. gave a better result than N.S. in nine trials of 1 pint and in eight

trials of 2 pints. However, in the remaining trials, the results showed either equality of effect or a strong reversal. The individual percentages in Table 3 were therefore converted into angles following Snedecor (1953, §16.7, pp. 447-8) and an analysis of variance (treatments, occasions and error) was carried out on the data thus transformed. This analysis gave $F = 3{\cdot}17$ for 3 and 33 d.f. when the variances for treatments and error were compared. The relevant differences to be tested for significance are A-B, C-D, A-C and B-D (see column headings in Table 3). Only one, A-C, is significant ($P = 0{\cdot}03$) and that is the difference of the results from using 1 pint N.S. and 1 pint D.S. The parallel comparison of strengths, B-D (2 pt N.S. and 2 pt D.S.) fails to be significant mainly because of the inordinately large contribution to the mean of D arising from the last entry on 27 July (100% = 90° concerning only two leatherjackets, one of which was a pupa!).

(*e*) *Discussion*

The experiment described in the last section was a preliminary exploration, and should be repeated with at least two turves per treatment on each occasion between the beginning of November and the end of April—not much later because leatherjacket numbers become too small and, besides, the efficiency of St. Ives fluid is then too low to be of interest. This might well confirm the hint that efficiency is increased somewhat by doubling the volume of fluid applied as well as by doubling the strength. To us, a dosage of 1 pint per square foot has always seemed inadequate, particularly when there is a dense mat to absorb most of it before it reaches the soil. That 1 pint is as successful as it is, may mean that leatherjackets are living most of the time just below the surface of the soil or even in the bottom of the mat, but there is as yet little or no knowledge available on this question.

GENERAL DISCUSSION

The work indicates that the St Ives method has practically the same efficiency in all types of turf and the efficiency does not vary excessively during the period November to May. The method is therefore quite suitable for detecting at least the grosser relative differences between places at any particular time (November to May) or trends from year to year at a particular place. Where a really reliable estimate of absolute population is required, however, the numbers in sample turves should be determined by the hot water process which has been shown to be 100% efficient from November to May. This process, though more laborious than the St Ives method, is much less laborious than turf-washing, the only other method with 100% efficiency.

With populations as high as at Spout Bank in 1955-56, a sampling unit of 6 × 6 in. is sufficiently large, and lessens labour. Partitions have now been fitted to the apparatus shown in Fig. 1 so that four 6 × 6 in. turves can be processed in the time necessary for one square foot. The apparatus can also be adapted to take nine 4 × 4 in. turves at once. A smaller sampling unit would probably be inadvisable.

Leatherjackets are by no means the only inhabitants of the turf (soil and mat) which surface in the hot water process. Earthworms (always first), enchytraeids, beetles, insect larvae, spiders, mites, slugs and snails, in fact all animals with the necessary motive power and open access to the surface, emerge hastily. Even the smallest, such as mites, betray themselves by the agitation of their movements arising from increasing discomfort. Workers interested in any turf-dwelling animal which has access to the surface might profitably look into the possibility of adapting this process which works so well with leatherjackets.

Apart from refinements necessary for collecting fragile enchytraeids, Nielsen's (1953) technique and our hot water process are essentially the same. Ignorant of his work but with the same basic idea, we developed our process independently.

SUMMARY

1. A method of determining numbers of leatherjackets (larvae of the *Tipula oleracea* group) on sample turves, the *hot water process*, is described. This consists in driving leatherjackets to the turf surface by means of heat carried by water rising through the turf. The method was developed independently, in ignorance of Nielsen's (1953) technique for enchytraeid worms.

2. From mid-October until the first prepupae occur, usually in June, the hot water process brings up all leatherjackets inhabiting turf, *i.e.* has 100% efficiency. After prepupation starts in the population and until emergence is complete, usually September, the efficiency drops, but not more than 5-10%.

3. The hot water process has been used to check the efficiency of the St Ives method of determining leatherjacket numbers. The latter method consists in bringing leatherjackets to the surface by means of an irritant emulsion of orthodichlorobenzene poured on the turf in the field after cutting the grass close.

4. Leatherjackets surface from 15 sec to 13 min after application of St Ives fluid. If left alone, some re-enter the turf, and others remain on the surface for up to 20 min. Hence observation must be continuous for 10-15 min after applying the fluid, and leatherjackets must be counted and picked off as they surface.

5. The efficiency of the St Ives method is about 85%, from November to May, then falls steeply to near zero in July.

6. Experiment suggests that doubling the strength or the volume of fluid should increase the efficiency of the method a little, but this requires confirmation.

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THE ECOLOGY OF EARTHWORMS IN CATTLE-GRAZED MACHAIR IN TIREE, ARGYLL

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(With Plate 1 and 3 Figures in the Text)

In a discussion of the distribution of the Lumbricidae in the shell-sand-peat complex of the Hebrides (1957a), and later in a detailed description of the distribution on a dune-machair (mature maritime grassland) transition in Tiree, Argyll (1957b), Boyd has drawn attention to the effects of naturally deposited bullock droppings on the species complex. These effects are now more thoroughly investigated in an area in the island of Tiree, Argyll, where the ground is flat, grazed only by cattle, and where the soil, vegetation and drainage are highly uniform. By selecting such a uniform type of habitat it was hoped to eliminate other large-scale ecological variation, and outline clearly the effect of the dung.

Evans & Guild (1947, 1948b) discussed the seasonal abundance of some British earthworms including two species present in the population now under examination, and (1948a) the reproductive cycle of several species including two present here, relating all to temperature and moisture content of the soil. The seasonal abundance and reproductive cycles of the machair population in Tiree are examined here and comparisons drawn with the findings of Evans & Guild.

METHODS AND MATERIALS

The problems of earthworm sampling in this area discussed by Boyd (1957b), connected with quadrat size, low faunal density, and availability of a copious supply of fresh water for the 'wet' method (Evans & Guild 1947), also apply here. The quadrat size selected was 1 m^2, and the 'wet' method of extraction used. Svendsen (1955) found that the 'wet' method was unsuitable for comparative studies of different earthworm populations, but in this case it seemed suitable, owing mainly to the shallow, porous and uniform nature of the soil. No attempt at achieving absolute numbers was intended, only monthly comparisons of the same population in the same habitat by a standard method of sampling. Unfortunately complete standardization was difficult to achieve because, when grazing ceased, the swards increased in height, and keener vigilance was necessary at each quadrat as the non-grazing season (June to November) advanced. Nine litres (2 gal) of potassium permanganate solution (14 g in 9 l. of water) were applied to each quadrat, the supply of fresh water being obtained about 50 m from the sampling area.

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The same procedure was followed each month for the period from November 1954 to November 1955. Twenty samples were taken at random within the survey area on different ground each month. Ten of these were taken excluding dung-pats from the quadrat (open soil), and ten including one dung-pat. The dung-pats were chosen randomly by casting the metal quadrat square and choosing the nearest pat. Very new and very old pats were not used, and in the case of suspected bias the

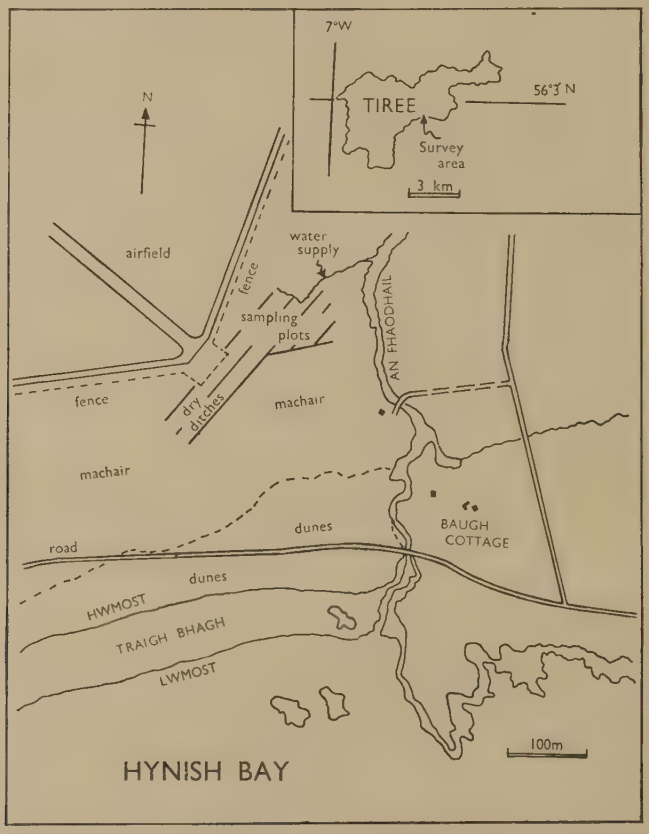

Fig. 1. Map of the survey area at the Reef machair, Tiree, showing the position of the sampling plots.

square was recast. The dung-pat frequency was measured every two months throughout the grazing season (December to May) in 12 × 12 m quadrats.

The earthworms were extracted from quadrats containing a dung-pat by first breaking up the pat with forceps, and then by the administration of the permanganate solution. The earthworms were preserved in 4% formalin for identification and counting according to the key compiled by Cernosvitov & Evans (1947). In some cases the immature worms could not be identified to the species; they were allotted

A vertical section of machair soil beside a ditch. The three layers are: *Top* – a soil formed from the throw-out from the ditch excavation, probably less than 50 years old; *Middle* the original soil compressed to about half the depth possessed in the absence of the superincumbent layer; *Bottom* the sand with traces of plant roots. The rule is graduated in inches

(*Facing p.* 149)

to the most closely related species according to the proportions of mature specimens of each species present. For taxonomic reasons described by Boyd (1957b) three species, *Bimastus tenuis*, *Dendrobaena rubida* and *D. subrubicunda* are included in one species complex.

THE HABITAT

The site is situated on a tract of mature maritime grassland (machair) about 250 m landward from a range of coastal dunes of highly calcareous shell-sand in Tiree, Argyll, and close to station 5 of the dune-machair transition described by Boyd (1957b), Fig. 1. The grassland is flat, possessing no large-scale undulations and broken only by a system of widely separated parallel ditches, which are usually dry, except during winter rains. The broad sections between the ditches possess, in the selected area, a uniform sward and what appears to be a highly uniform soil, which is an organic mould and shell-sand mixture of very fine grain, and forms a shallow mat on top of the sand (Plate 1). The soil has never been tilled, and the vertical discontinuity between it and the sand is sharp, occurring usually at a depth of about 15 cm. The pH of the soil was 7·6 to 7·7, the $CaCO_3$ content 55 to 60% dry weight, and loss of weight on ignition (at 500° C for 18 h) 11 to 15% dry weight. The vegetation is similar to that listed by Darling (1947) for machair, and contains no *Ammophila arenaria*. The fauna includes the long-tailed field-mouse (*Apodemus sylvaticus* (*hebridensis*?)), pigmy shrew (*Sorex minutus*), lapwing (*Vanellus vanellus*), starling (*Sturnus vulgaris*), gulls (*Larus* spp.), golden plover (*Pluvialis apricaria*) on migration, and several species of beetle. All these probably prey on earthworms. The rabbit (*Oryctolagus cuniculus*) is absent from Tiree, but the hare (*Lepus europaeus*) is present.

SPECIES DISTRIBUTION

In describing the earthworm community of machair soils, Boyd (1957a) points out that species differ in their preferences for niches such as open soil, in and under dung-pats, and under stones. In this paper, samples taken from the spaces between dung-pats are said to be taken from 'open soil' (grass), and samples taken from under, in, and in the immediate vicinity of a dung-pat, from 'dung-pat'.

Allolobophora caliginosa was found to be significantly more abundant in open soil than in dung-pats, while the opposite was found to be the case with *Dendrobaena octaedra* and *Lumbricus rubellus*. These are the three dominant species on grazed machair. When investigating the distribution of species in areas such as machair where the earthworm fauna is light and samples are taken both from open soil and dung-pats, it is probable that not enough samples are taken from open soil to offset the concentrating effect of the dung on *Dendrobaena octaedra* and *Lumbricus rubellus*, and to bring out the diffusely scattered *Allolobophora caliginosa* in truly representative numbers.

The numbers obtained from two sets of samples between November 1954 and

November 1955 are given in Table 1. In the cases of *Allolobophora caliginosa*, *A. chlorotica*, *Dendrobaena octaedra*, *Lumbricus castaneus* and *L. rubellus*, the difference between the total for each niche is seen to be significant ($\chi^2 > 3{\cdot}841$), and insignificant in the case of the *Bimastus-Dendrobaena* complex, *Octolasium cyaneum* and *O. lacteum*. *Allolobophora caliginosa* is affected in a way contrary to *Dendrobaena*

Table 1. *Total collections of earthworms taken from quadrats each containing one dung-pat, and quadrats in the spaces (open soil) between the dung-pats*

The data are taken from twenty samples (1 m²) each month for 12 months, half of which were taken with a dung-pat and the other half in the spaces. S, significant ($\chi^2 > 3{\cdot}841$); N/S, insignificant.

	Open soil	Dung-pat	Difference
Allolobophora caliginosa Savigny	439	277	S
A. chlorotica Savigny	3	12	S
Bimastus tenuis Eisen *Dendrobaena rubida* Savigny *D. subrubicunda* Eisen	5	12	N/S
D. octaedra Savigny	22	101	S
Eiseniella tetraedra Savigny	0	0	S
Lumbricus castaneus Savigny	1	65	S
L. rubellus Hoffmeister	53	456	S
Octolasium cyaneum Savigny	8	5	N/S
O. lacteum Orley	1	0	N/S

octaedra and *Lumbricus rubellus* confirming the previous observations of Boyd (1957a). The dung-pat frequency on the Reef machair taken from 12 × 12 m quadrats at intervals of 2 months throughout the grazing season, December 1954 to May 1955 inclusive, ranged from 11 to 19 (mean $13{\cdot}6 \pm$ S.D. 2·99) in December and January, from 15 to 28 (mean $18{\cdot}5 \pm 4{\cdot}04$) in February and March, and from 13 to 30 (mean $21{\cdot}5 \pm 4{\cdot}81$) in April and May. As might be expected the frequency

Table 2. *The relative abundance in April and October 1955 of* Allolobophora caliginosa, *and* Lumbricus rubellus *in machair soil grazed by cattle*

The data are taken from twenty samples (1 m²) each month, ten of which were taken with a dung-pat included in the quadrat and the other ten in the spaces (open soil) between dung-pats.

		Allolobophora caliginosa		*Lumbricus rubellus*	
		Dung-pat	Open soil	Dung-pat	Open soil
Frequency of dung-pat and open soil in quadrats of 144 m²		22	122	22	122
Earthworms/10 m²	April	57	67	63	0
	October	27	46	11	6
Earthworms/144m²	April	942·8		138·6	
	October	620·6		97·4	
Ratio of numbers, *A. caliginosa* / *L. rubellus*	April	6·802			
	October	6·372			

increases fairly uniformly throughout the season. Table 2 combines earthworm and dung-pat distribution. The dung-pat frequency for the period April-May 1955 is used to divide the 12 × 12 m (144 m²) into 122 m² without dung, and

22 m² with dung. The dung-pat frequency in October, when the pats are degenerate, would be approximately that of April-May, none having been added in the intervening period and none having completely disappeared.

By simple multiplication and addition figures (6·802, 6·372) are obtained which are not intended in any way as absolute numbers, but as indices for comparison of species strength. These figures might only apply to the highly uniform type of

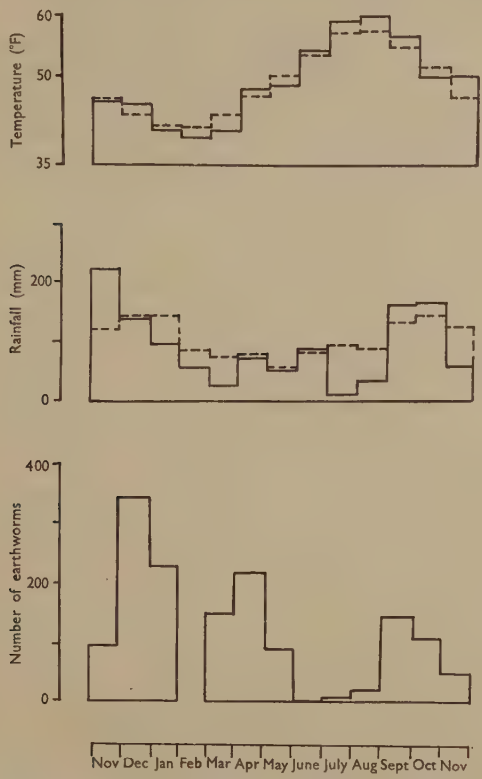

Fig. 2. The total numbers of earthworms (all species) collected from twenty samples each month from November 1954 to November 1955, together with air temperature and rainfall data. The mean figures for the period 1943-52 (broken line) are given to show abnormal conditions in 1954-55 (full line).

machair over which this sampling was done. It does not present an ideal case, however, since the shape, size and quality of the dung-pats, some of which may have been searched by birds, varies. It is clear, however, from the figures obtained towards the end of the grazing season (April) and towards the end of the non-grazing season (October), that *Allolobophora caliginosa* is more numerous throughout the population of the grazed machair than *Lumbricus rubellus*, the suggested

figure being six or seven times as great. It is much more numerous still than *Dendrobaena octaedra*. Reynoldson, O'Connor & Kelly (1955) found *Allolobophora caliginosa* to be more numerous than all other species of earthworm in the soils of a raised beach and permanent pasture on Bardsey Island, North Wales. Dung-pats were searched, but the effect of these on the distribution of the species is not discussed. Reynoldson (1955) has also shown that in permanent pasture close to the sea in North Wales, *A. caliginosa* is numerically dominant to all other species.

The sampling area was not grazed between 27 May and 27 November 1955. During the growth of the sward throughout the summer and autumn, observations were continued in order to detect any possible decline of the influence of the dung-pat on the earthworm population. From Fig. 2, showing totals of twenty samples each month for 12 months (February excepted) together with air temperature and rainfall figures obtained from a meteorological station about 1 km from the sampling plots, it is seen that owing to unusual heat and drought practically no earthworms could be obtained by the 'wet' method during the period June to August though in June rainfall and temperature were about average. The decline in numbers was so sharp as to defeat attempts at tracing a fall-off in numbers with the decay of the dung-pats, which became as hard as stone. At the height of the drought the soil dried out to a depth of about 8 cm, and below that level the earthworms were curled up and inactive.

Comparisons between numbers of *Allolobophora caliginosa*, *Dendrobaena octaedra* and *Lumbricus rubellus* at the end of April when the effect of the dung-pats would be thought to be approaching maximum, and in mid-October when the effect would be approaching a minimum show significant differences. The diffuse distribution of *Allolobophora* is sustained both in April and October, while the cluster distribution in the dung-pats in the other two species in April appears to have broken down by October. The differences between numbers of *A. caliginosa* from ten samples of 1 m^2 with a dung-pat, and ten samples of 1 m^2 without a dung-pat was not significant in April ($\chi^2 = 0{\cdot}806$), but was just significant in October ($\chi^2 = 4{\cdot}945$). Those for *Dendrobaena octaedra* were highly significant in April ($\chi^2 = 26{\cdot}133$), and not significant in October ($\chi^2 = 3{\cdot}000$). Those for *Lumbricus rubellus* were highly significant in April ($\chi^2 = 63{\cdot}000$), and not significant in October ($\chi^2 = 1{\cdot}471$).

The presence of dung-pats is seen to affect greatly the distribution of the earthworm population, all species probably being affected to a different degree. The dung-pat may be considered as the focus of an earthworm community distinct from, yet primarily derived from, the background complex of the field population.

ABUNDANCE

Evans & Guild (1947, 1948b) estimated the abundance of five species of earthworm in agricultural fields in England. The sampling method used was the 'wet' method, which has been adversely criticized by Svendsen (1955). The vertical movement in such old-established agricultural soils is probably great, and much

greater than in machair soil (Boyd 1957a). Stephenson (1930) summarizes information by Darwin and others about the depth to which earthworms penetrate in winter. It is generally accepted that they penetrate to deeper levels where the temperature is higher and more constant. The main body of the population is not at constant depth, and this would be expected to affect the catch obtained from a standardized 'wet' sample. In Tiree, however, the depth to which the population penetrates is fairly constant, from the surface to about 15 cm (Boyd 1957a), and always well within the effective penetration of the solution. Comparisons between the two investigations will therefore be of interest.

Fig. 2 shows the monthly fluctuations in the total earthworms of all species collected from twenty samples each month. No sampling by the 'wet' method was possible during the visit in February because of frost, but by breaking the thin frozen crust with a spade, earthworms were seen to be fairly numerous and active from a depth of 5 cm to the sand at 15 cm. The annual cycle of abundance of this population reaches a peak in December, declining gradually to a trough from June to August, with a secondary peak in April. This is somewhat similar to the findings of Evans & Guild (1948b). During the summer in question a great proportion of the population in the grazed machair soil probably died in the extraordinary drought. Few earthworms were obtained by the 'wet' method. This was not entirely due to the failure of the population in a state of suspended animation to respond to the chemical stimulus, for digging showed that comparatively few were in fact present. Numbers rise to a secondary peak in September, but before rising to the primary winter peak there is a trough in November.

All the features of the annual cycle shown by Evans & Guild (1947, 1948b) are found also in this work. Small variations, however, occur in the times of peaks and troughs, the most obvious being that of the autumn-winter peak. The reasons advanced by them in explanation of these fluctuations in numbers, involving predation, emergence from seasonal quiescence, the emergence from cocoons, and the effects of limiting moisture content of the soil, seem satisfactory when applied to the present situation. The mid-winter trough shown by Evans & Guild is perhaps deeper in mainland populations than in maritime populations such as that in machair soil, owing probably to the comparatively mild Hebridean winters. The mid-summer trough in this case is probably accentuated by the drought, and is no doubt shallower than that on the mainland due to the comparatively wet Hebridean summers (Manley 1948).

REPRODUCTION

In a study of the life-cycles of British Lumbricidae, Evans & Guild (1948a) examined the reproductive cycle by measuring cocoon production in laboratory cultures. In a complementary work on field populations (Evans & Guild 1948b) they show seasonal trends in populations of immature, adolescent and sexually mature earthworms. The percentage of mature earthworms (with a clitellum) present in monthly 'wet' samples from November 1954 to November 1955, are

used here to trace the annual reproductive cycle of the population in machair soil at the Reef, Tiree.

Before comparing the cycles observed by Evans & Guild and those observed in Tiree, Fig. 3, it must be emphasized that the two cycles, though comparing two closely related attributes, viz. numbers of cocoons with percentages of mature earthworms, do not compare the same attributes of the population. Cocoon data were obtained from laboratory cultures with the temperature varying naturally,

Fig. 3. The percentages of mature earthworms in the monthly catches for the period November 1954 to November 1955.

but with the moisture content always optimal, and the mature earthworm data were obtained from the sampling of a natural population in natural conditions. Evans & Guild found that the species can be divided into those which have continuous production of cocoons throughout the year following closely the soil temperature gradient, and those which have a reproductive pause during the summer. All the species, except *Allolobophora longa* and *A. nocturna* Evans, including five found in this particular population in Tiree, are shown by Evans & Guild to have uninterrupted reproduction throughout the year in optimal moisture con-

ditions. Although production differed between soils of different types, it ceased between soil moistures of 15 and 20% of the dry weight of the soil. Unfortunately no comparable graphs for the moisture content of the soil such as those for temperature are given by Evans & Guild, since moisture content was not measured as a natural variation over the space of a year, but was controlled in a replicated experiment, in which several moisture levels were maintained simultaneously for 43 days.

Fig. 3, shows the monthly percentages of mature earthworms obtained from the total monthly collections. The overall percentage is broken up to show those of *Allolobophora caliginosa*, *Lumbricus rubellus*, and all the other species considered cumulatively. Temperature and rainfall data are also shown (Fig. 2).

The period of this sampling programme included the extraordinarily dry spring and summer of 1955, when air temperatures remained normal and rainfall values from December 1954 to August 1955 inclusive, except June, were well below the normal. In contrast to the results of the cocoon counts by Evans & Guild, maximum reproduction appears to take place in the machair population during the winter and not in summer, the peaks and troughs being reversed. The percentages of *Allolobophora caliginosa*, *Lumbricus rubellus*, and the other species considered cumulatively show similar tendencies. No result was obtained for February 1955 because of hard frost prevailing at the time of sampling.

Evans & Guild (1948b) show, however, that the strength of a field population is lowest between May and August in the south of England, when numbers of sexually mature individuals are also at a minimum. It follows that the reproductive cycle of a field population is not similar to that shown by the cocoons produced by a laboratory culture at optimal moisture levels. The peak shown by Evans & Guild (1948a) may not in fact exist in British field populations where reproduction is influenced by variation in soil moisture. It is probable that it does not exist even in the comparatively moist and cool situation in Tiree since there were no sexually mature individuals found in the grazed, and few in the ungrazed swards, in the dry season.

The peak occurred between November and January when the mean monthly air temperature ranged from 45·5 to 40·9° F, the seasonal trough, and the monthly rainfall ranged from 225 to 96 mm, the seasonal peak. In February the mean monthly temperature was 39·3° F and although the frost precluded sampling during that month it did not last for more than a few days, and at worst the soil was only frozen to a depth of 5 cm, extraordinary freezing in Tiree. The frozen crust was broken by a spade and below the earthworms were found to be plentiful and active, many mature worms being noted. Between April and May a distinct ecological threshold had been crossed, and the numbers of mature worms in the population had dropped almost to zero. Such a threshold is mentioned by Stephenson (1930) in the sudden disappearance of earthworms with clitella from a North American population subjected to a sudden spell of cold weather in autumn. In this case, however, there is no apparent temperature threshold, but a possible moisture one. A similar threshold would seem to be crossed in the opposite

direction to that of April-May, between September and October. At this time the rainfall (Fig. 2) increased greatly with a corresponding increase in the number of clitellum-bearing earthworms in the population. The abnormal weather conditions discussed above also apply in this connection. During July and August the soil was very dry to a depth of 8 cm, and no clitellum-bearing earthworms were found in the sampling plots either by the 'wet' method, or by digging.

Monthly fluctuations in the percentage of mature worms in the population follow closely those of total numbers (Fig. 2). The autumn peak shown by Evans & Guild (1948b) in English populations occurs in advance of the corresponding peak in Tiree, and the trough between January and March is less distinct in the machair population.

ACKNOWLEDGMENTS

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SUMMARY

1. The soil habitat of mature maritime grassland (machair) at the Reef, Tiree, Argyll, is briefly described.

2. The effects of naturally deposited bullock dung on species distribution are discussed. *Allolobophora caliginosa* is seen to be affected in a manner contrary to *Dendrobaena octaedra* and *Lumbricus rubellus*, both of which were found aggregated in or under the dung-pats.

3. The annual cycle of abundance (measured by fluctuations in total numbers in monthly samples) reaches a peak in December, falling to a trough from June to August, with a secondary peak in April.

4. The reproductive cycle (measured by fluctuations in percentage of clitellum-bearing earthworms in the monthly samples) reaches a peak from October to January and a trough from May to September, with a sharp fall in May and an increase in October.

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REVIEWS

REFLECTIONS OF AN ECOLOGIST

A. Macfadyen (1957). *Animal Ecology: Aims and Methods.* Pp. xx+264; 6 plates; 19 text-figures. London: Pitman. Price 40*s*.

On p. x the author lists ten subjects with which the ecologist should be acquainted; unkind readers will add an eleventh—English. The style is rough, with many superfluous words, ugly constructions, and small errors of the kind that has provoked in recent years the writing of several books on the correct use of English. Original papers are referred to by numbers. Occasionally there are strings of references which, if indicated by authors' names and dates in the conventional way, would occupy space and break up the text, but they are not numerous enough to outweigh the two objections to the system well illustrated by this passage on p. 222: ' ... has been criticized by the Scandinavian authors (1, 2, 3, 4)'. The reviewer, familiar with the controversy and curious to know who else had joined in, turned up the reference list, only to find that all four papers are by one person after all. Had the usual system been employed, the author would not have made a mistake, trivial in this instance but baffling when he misquotes a number (*e.g.* p. 165), and the reader would not have had to break the thread of the text to look up something already known to him.

The preface describes the plan of the book and should be read; it might indeed have been wiser to call it Chapter 1. The actual first chapter stresses the importance of taxonomy and mentions briefly the fields where taxonomy, genetics and studies of evolution overlap. With a thin chapter on the relations between animal ecology and vegetation, one on microclimates which does not logically belong, and two in which the author develops his ideas on the study of ecology, it forms Part I of the book. Mr Macfadyen distinguishes 'scientific natural history' from true 'ecology' or 'autecology' from 'synecology' though aware that clear-cut distinctions remain elusive. Real ecology is any study of all the animals whether they be flour beetles in a tube or the inhabitants of a piece of soil cut out by a sampler, and the second and third parts of the book are devoted to it. Physiologists who study tolerance ranges and preferenda in laboratory experiments, and those who try to define the habitat of a species by observing its occurrence in the field are disposed of in Part I, in that order, illogical to the reviewer, who has always looked on the laboratory experiment as the natural sequel to field observation. Undoubtedly some experimental zoologists have produced worthless work because they failed to take into account all the factors influencing the animals under observation, and undoubtedly this complexity presents difficulties, but they are not insurmountable. The author seems too obsessed with the difficulties and unacquainted with some of the more notable achievements. The field naturalist is handled more kindly but in this chapter also I have the impression that the difficulties receive undue emphasis. Possibly Mr Macfadyen is seeking to justify his approach to ecology, in which case he is doing something that few will think needs doing. The subject is diffuse and anyone aiming to write a stimulating book with a continuous theme must select one aspect of it. Moreover, limiting factors in ecology rarely act like brick walls; generally conditions become progressively unfavourable and, before the lethal point is reached, a species disappears because it cannot breed fast enough to make good losses or because some similar species can produce greater numbers at that level. Disappearance is therefore not due immediately to intolerable physical or chemical conditions but related to numbers. There must, therefore, be a mathematical basis to the subject. The presentation of this mathematical background

is the main task that Mr Macfadyen has set himself and he has accomplished it very well.

The worker who wishes to define and distinguish communities must know the relative numbers of each species but need not be too concerned about absolute numbers per unit area; his main burden is putting names to all his species. On the other hand, the worker whose interest is the relations between populations will study a few abundant species only and his taxonomic troubles will be small; exact knowledge of numbers, however, will be important. How large each sample should be and where and when it should be taken are questions which must be answered with moderate accuracy at least at the outset of a survey. Within the space of one chapter no author can give more than general instructions, a warning about pitfalls and a list of the main references, though in places, and not in this chapter only, the reader will regret that Mr Macfadyen, who has clearly thought deeply about sampling, was not able to find space for a few examples to illustrate his points. If the sex and age of each animal in a sample are noted and information about breeding in the species is available, the numbers that the population could reach in a given time if they were not checked can be calculated. Two formulae for doing this are presented in Chapter 8, their relative merits are discussed, and it is shown that the exercise is not purely academic, for rates of increase not far short of the possible may occur when grain pests find a new store or rats a new corn-rick. The chapter ends with a short explanation of exponentials which, together with several other similar interpolations, may annoy the few who know the subject already, but is likely to be welcome to many readers.

Food chain studies lead to a consideration of production, introduced by a remarkably thorough discussion of the way in which English- and German-speaking workers have used various terms, and some examples of reasonably complete calculations of production are briefly described. Any assessment of the efficiency of production demands a knowledge of the flow of energy through a community, which could be calculated if it were known how fast each species consumes oxygen and how the rate varies with size and temperature. It would of course be necessary to sample the population frequently and to count and measure the animals, as well as to keep a record of the temperature and to observe whether the animals moved up or down to maintain themselves in any particular part of the steep temperature gradients that can be set up in soil. It is not surprising to find that this is one of the fields in which ecologists have left undone those things that they ought to have done.

Part 3 starts with a excellent historical account of views about how animal numbers are controlled, and continues with description and illustration of the three lines of approach, mathematical theory, laboratory experiment and field observation. The conclusion is that ultimately control is always due to some density-dependent factor and that numbers of a species may be limited by a competitor, a predator, a parasite or by itself, changes brought on by crowding causing numbers to drop before the effect of a density-dependent factor can increase significantly.

Finally there are two chapters about the community, one on how to delimit it in the field, the other on what it is, or rather on what various workers have thought that it is, and two concluding chapters. The first points out some of the practical applications of ecological research and dwells on fields in which it has been ignored; the second is a brief summary of the book with a forecast about future trends.

Even the mathematicians do not always agree and, as the author points out, the simplest experimental system often proves much more complicated than appeared possible at first. The field will, therefore, remain a scene for debate and disagreement and bricks will fly around for many years to come. Some will land on Mr Macfadyen's head. He will, however, be used much less as a target than as a source of ammunition. He has written a carefully thought-out book on the ecology that springs from mathematical theory, and presented fairly its implications and its applications. I hope that not too many people

will accept his contention that this is the one true ecology, because that is an attitude which, whether in religion, politics or science, has always led to the discouragement of original thought, but I am sure that this will be one of the important books on the ecologist's bookshelf for some time to come.

T. T. MACAN

FISH PHYSIOLOGY

Margaret E. Brown (Editor) (**1957**). *The Physiology of Fishes:* Vol. I. *Metabolism.* Pp. xiii+447; numerous text-figures. New York: Academic Press. Price $12.00.

This book together with Vol. II, when published, is the first attempt at a comprehensive survey of the physiology of fishes. That such a survey has been attempted and that it should fill two volumes is an encouraging reflection of the amount of interest shown today in fish physiology, and the progress that has taken place in our knowledge of the subject in the last 25 years. Vol. I is composed of the following ten chapters. The respiration of fish by F. E. J. Fry with an account of air breathing in fish by G. S. Carter: The Cardiovascular System by J. C. Mott; The Alimentary Canal and digestion by E. J. W. Barrington; Secretion and Osmoregulation by V. S. Black; Skin and Scales by J. van Oosten; Endocrine Organs and the Gonads and reproduction by W. S. Hoar; Early development and hatching by S. Smith; Experimental studies of growth by M. E. Brown; and The Biochemical Composition of fish by R. M. Love.

The authors are to be congratulated on this comprehensive account of the literature; as a reference book this volume will be of immense value both to research workers and students interested in this subject. It would, however, have been of greater value to these workers and of greater interest to all zoologists, particularly to ecologists if the original scope of the book had been wider. W. S. Hoar in his excellent account of the Endocrine organs expresses on p. 266 what should have been the aim of the whole book when he says 'there are so many tantalizing and baffling problems in the metabolism of fishes that this section may not be out of place as à stimulant to research'. How much more stimulating this book would have been if it had not taken the form of a straight review of the results of research but rather of a critical appreciation of these results coupled with speculation on their interpretation. Surely authors in a book of this kind should be encouraged to indulge in imaginative speculation. The gaps in our knowledge could well have been more clearly indicated and above all the inter-relationships between physiology and other zoological studies emphasized. The chapters on respiration and osmoregulation admirably illustrate this last point for they will profit all ecologists who read them.

There is only one statement in the book which I feel cannot be left unquestioned. On p. 218 van Oosten talks of dissolved minute particles of regurgitated food being absorbed through the skin of goldfish. To talk of 'dissolved particles' displays, I feel, a certain amount of confused thinking and to suggest on the evidence on which I feel this statement is based, that these 'particles' are absorbed through the skin is very dangerous. Perhaps he has fresh evidence on the subject, but unfortunately as he gives no reference at all during the whole of his chapter, it is impossible to tell.

This book then is an extremely useful and competent review which despite its high price is essential for the library of any worker on fish problems. It fails, however, to make the most of its opportunities, and instead of pointing out new and interesting paths of discovery for the most part contents itself with the dry reiteration of published data with little attempt at a critical assessment of their value.

D. R. SWIFT

AN ENTOMOLOGICAL CLASSIC

A. D. Imms. *A General Textbook of Entomology.* Ninth edition entirely revised by **O. W. Richards** and **R. G. Davies** (**1957**). Pp. x+886, 609 text-figures. London: Methuen. Price 75*s*.

The *General Textbook of Entomology* has been the standard reference work now for over 30 years. Its clarity of style and excellent balance between generality and useful biological detail was the foundation of its popularity, and it passed through eight editions during the life-time of the author. Professor O. W. Richards and Mr Davies have undertaken the herculean task of a complete revision; the type has been entirely reset, which has permitted both extensive changes where necessary, and detailed changes on almost every page. As a result the book has been brought substantially up to date in every respect, and has been given a new lease of useful life.

The first part, on insect anatomy and physiology uses similar chapter heads to the earlier editions, but revision here has been particularly thorough, and has greatly strengthened what had become perhaps the least up-to-date part of the book. New sections have been added on such topics as nutrition, digestion, the respiratory system, and the endocrine glands, making this part some 30 pages longer than formerly.

The second part, on development and metamorphosis, has increased in size from 30 to 45 pages, and gives many references to work published since the previous edition.

The third and largest part deals with the classification and phylogeny of insects and has expanded from 473 to 582 pages. Although the biological details which are so useful in this work remain without great changes, many new facts and references are included and they have been reorganized to conform with more modern views on insect classification. On the whole the revisers have shown excellent judgment in steering a course between old-fashioned lumping, which tends to hide structural and biological differentiation, and the modern taxonomists' trend towards undue splitting, which obscures relationships and results in insect orders, like the Grylloblattodea, including but a single genus.

The number of orders recognized has risen from 23 to 29 by the separation of Diplura from Thysanura, the subdivision of Orthoptera into four, and the separation of the biting from the sucking lice. In the endopterygote orders the revisers have been mercifully conservative. However, revision within the Coleoptera has been extensive, following the studies of Crowson, and in the Lepidoptera the basic subdivision recognizes the importance of female genital systems (stressed by Hinton and others) whilst retaining and extending the important superfamily distinctions based on the tympanum and wing venation, as advocated by Imms. The Diptera have remained basically as in recent editions apart from the transference of families Braulidae, Gasterophilidae and Cordyluridae to more appropriate positions, and the recognition of many new families amongst the Acalyptratae. The longstanding confusion in naming wing veins has at last been put right. The Hymenoptera have been rearranged to a considerable extent, and a new key to the classification is provided which should work moderately well. It is a pity that the character used to separate sawflies from Apocrita remains unchanged from earlier editions, as beginners will continue to mistake some chalcid wasps for sawflies.

Three improvements in the new edition are worthy of comment. All the keys, so useful to ecologists, have been rearranged so that contrasting couplets are adjacent to each other, and most have been rewritten to include more families. The references have been given in the more convenient standard form, and include titles. Lastly the author and subject index have been combined, and whereas they occupied 32 pages each with two columns, now they spread over 54 pages with three columns, and the number of entries has been greatly increased. Whether it is big enough yet is open to question, as a surprising

number of genera referred to more than once in the text have only a single-page citation in the index.

These criticisms are minor ones. The book is so different from the previous editions that both libraries and individuals will be well advised to have it available. The revisers are to be congratulated on completing their task so successfully.

G. C. VARLEY

POND LIFE FOR THE AMATEUR

W. J. Prud'homme van Reine (1957). *Plants and Animals of Pond and Stream.* Translated from the Dutch and adapted for use in Great Britain in collaboration with Mona C. Harrison. Pp. vi+159. 34 plates (8 in colour). London: Murray. 12*s.* 6*d.*

Readers who are parents or teachers in schools may be interested in this book, which consists of illustrations and descriptions of some 500 animals and plants found in or near fresh water. The pictures are good but the best use has not been made of the text; it is extremely difficult to give a valuable description of a species in five or six lines, and hardly any space is devoted to accounts of the general features of groups. This arrangement has the defect that, if a reader's specimen is not illustrated, the book does not help him. For example, the whole of the Order Trichoptera is represented in the larval stage by two species, both making cases of vegetable material, and there is nothing that would enable the captor of a net-spinning species to do more than assign it to the right class. Moreover, if he does find a picture that his specimen resembles, the user of the book does not know whether he has the species illustrated or a closely related one.

The potential buyer will expect to be told by a reviewer whether his book has something that no other has and, if not, how it compares with its rivals. The obvious comparison is with Clegg's *Observer's Book of Pond Life* (Warne). The purchaser of the book under review would pay two and half times more than he would for Clegg's and for that he would get larger type more generously spaced and about 100 more illustrations, most of which, however, are not of strictly aquatic species, for 60 birds and many plants occurring near water are included. Actually the genuine fresh-water field is covered more thoroughly by Clegg, who has made a better selection of species to be illustrated. He has also written a much more valuable text without the pitfalls mentioned above. The treatment of the water-bugs in the two books illustrates the difference between them. The pictures are almost exactly the same. Clegg devotes nine lines to a general description of the group and leaves his illustrations to speak for themselves. Against his no. 6 he writes 'Lesser Water Boatman. *Corixa.* 36 species'. Van Reine has no general remarks on the group and, in two pages of descriptions, conveys less of the really essential information. His caption is 'Lesser Water Boatman. *Corixa geoffroyi* Leach', with no indication that there is any other species, which is misleading.

T. T. MACAN

APPLIED ECOLOGY

Index of Agricultural Research (1957). Pp. xiv+189. Cambridge: University Press (for the Agricultural Research Council). Price 12*s.* 6*d.*

This is in fact three indices, one by research subjects divided into sections, one by animals and one by crops. A key to the abbreviated titles of institutions provides a convenient list of the laboratories and units supported by the Agricultural Research Council, and the whole is a useful guide to the applied ecological research in progress in Great Britain.

A TREATISE ON MAMMALS

J. Z. Young (1957). *The Life of Mammals.* Pp. xv+820; 338 text-figures. Oxford: Clarendon Press. Price 84*s*.

This is a text book of mamalian anatomy, physiology and embryology for students of zoology and for medical students. But it is much more than that, for it not only analyses but synthesizes knowledge derived from a vast field into a biology of the mammals in the widest meaning of the term. It presents the mammal as a living system and shows what an extensive understanding we now have of the almost incredibly complex structure of animals and of its equally complex manner of functioning. It also shows that all this has only begun the journey of exploration and that the road yet to be travelled seems to have no ending, although it takes us through scenery of ever-increasing fascination. The author points out that in due time we shall learn how to combine macroscopic and microscopic studies with those of biochemistry and biophysics, and modestly adds, 'All that I have been able to do here is to issue reminders that there is a connexion and to suggest possible means of unification.' The book incorporates the results of the latest researches that make use of the most modern methods, and illuminates the whole with a philosophy that emphasizes the self-regulatory and self-perpetuating nature that is the essence of living systems.

In a book of this scope, limited to 800 and odd pages, it is impossible to treat of 'many aspects of mammalian life that many would wish to study, for example ecology. It provides only a framework or scheme for the study of mammalian life, within which much else could be incorporated'. The author wisely refrains from attempting to fill the framework with details drawn from the great number of different kinds of mammals, and uses the rabbit and man to provide nearly all the examples and illustrations—the two species on which the readers to whom the book is primarily addressed will carry out their practical studies. The fundamentals set forth are, however, universal in application and can be extended and adapted indefinitely to any deeper study of mammals.

The essence of the book is contained in the first chapter, on 'The Control of Living Systems'. 'Animals may be said to remain alive by taking action that foreshadows or predicts the probable course of events. They can do this because the body, and especially the brain, contains a record of past sequences and associations. . . . As each individual life proceeds an increasing store of knowledge about probable sequences of events is built up and this is drawn upon in each new situation, so that actions that ensure survival can be made in circumstances that resemble those of the past.' Professor Young emphasizes that all living systems are homeostatic, and resist the tendency to diffusion into the surroundings that operate in all physical systems that differ from their surroundings. This leads to those activities that maintain the independence of the organism from the surroundings and are directed to the preservation of the system.

As Professor Young points out it is very difficult to make this concept of 'direction' precise, although without it no living organism can be adequately described. He suggests that it can best be expressed by saying 'in each situation the selection between possible actions of the living system is determined not only by the conditions obtaining at the moment but also by an information store or record of the actions that have ensured survival in the past under various sets of circumstances'. Information provided by heredity is coded in the genes, and acts from within to give certain tendencies that have been selected in past history. Events occurring in the environment, however, constantly modify these innate tendencies so that all tissues have a double dependence upon these two factors. Information stores of past individual experiences are not confined to the nervous system even in the higher animals, but are contained in all the tissues as 'adaptations' that improve the organism's representation of the environment and provide 'powers of action likely to be useful if the future resembles the past'.

Further comparison of living systems with man-made self-regulating machines develops the point of view that a living system maintains an improbable steady state that isolates it from its surroundings because its past history allows it to construct a representation of environmental conditions from the information it receives. The representation is used to assess any mismatch likely to destroy the steady state and, by a system of negative feed-back, sets controls into operation to maintain the stability. The numerous and varied controls may act rapidly as in the reactions that take place through the nervous system, slowly as in those produced by the hormones, or very slowly as in the adjustments involved in the process of evolution.

The author suggests with justice that his comparison of living systems with machines that control themselves is an advance in biological thinking. It enables the animal to be described as a whole in a way that has not been possible before, and provides the possibility of unifying the different treatments that are adopted by anatomy, physiology and all the other disciplines that make up the science. He points out that since the substance of the body is continually changing the old analogy of a simple machine with structure and function is no longer adequate. 'Comparison with machines that control themselves is much more helpful, especially if we can find ways of describing how the control system itself changes with time. The methods used by information theory may be able to do this because they tell us how to deal with situations that are controlled by the accumulated effects of associated events, some of them occurring long ago.'

After setting forth the point of view from which he intends to examine the life of mammals, Professor Young devotes nearly forty chapters to a consideration of the various parts of the mammalian body and combines anatomy and physiology, behaviour, genetics and many other aspects of the subject in the overall concept of homeostasis. Six further chapters deal similarly with development. This treatment is highly successful and brings the driest of dry bones very much to life so that, although the book is crammed with information and technicalities, it can be read with as much pleasure as any exciting story of fiction or adventure.

It would have been helpful to the student if Professor Young had been able to devote more space to the specific question of evolution, for at first sight homeostasis appears to be the antithesis of evolution. If homeostasis is the preservation of the individual from dissolution in a changing environment one can agree that when individuals differ some of them may be more successful than others in preserving themselves. 'Evolutionary change is produced by adjusting the hereditary make-up of the race by mutation, recombination of genes and natural selection. These processes provide an inherited information store that allows the organisms to make responses that are correct forecasts and thus to survive in the environmental situations that they meet.' But the hereditary information can only be inherited when there is no mutation; if a mutation occurs it is equivalent to an alteration in the coded 'message' carried by the genes. This may perhaps be one of the reasons why mutations, so far as is known, more often bring disaster rather than advantage—a vast number of fortuitously garbled messages must be sent before one turns up that accidentally makes sense. The cause of mutations in nature is unknown—some of them may be caused by cosmic ray bombardment—but, whatever their cause, they seem to arise from influences acting outside the organism. Small mutations cause fluctuations in the character of populations so that natural selection can act upon the species, and homeostasis can preserve the new characters that are advantageous.

Professor Young has written a most stimulating and valuable book that will be read with pleasure and profit not only by all those to whom it is primarily addressed but by all students of biology whether their examinations are long past or still to come. Is it too much to hope that it will be read by a wider public? The book shows that every biologist must have at least some knowledge of the fundamentals of physics and chemistry. It

is a disturbing thought that chemists and physicists can go through life from the cradle to the grave without the most elementary smattering of biology—without even being aware of its existence as a science. It would be an immense advantage if all chemists and physicists were required to read this book before taking their final examination; it would help them to attain both humility and humanity, and would enable them to adjust themselves to life more adequately—to take the first step towards fulfilling the philosopher's injunction γνῶθι σεαύτον.

L. HARRISON MATTHEWS

BOOKS RECEIVED

Insect Life in the Tropics by T. W. KIRKPATRICK. London: Longmans. 1957. Price 35*s*.

The Faunal Connections between Europe and North America by CARL H. LINDROTH. New York: Wiley, and Stockholm: Almquist & Wiksell. 1957. Price 120*s*.

Studies in Biology and its History. Vol. I, Ten essays by F. S. BODENHEIMER. Jerusalem: Biological Studies. 1947. Price $6.00.

Treatise on Marine Ecology and Palaeoecology. Vol. II, *Palaeoecology*, edited by HARRY S. LADD. New York: Geol. Soc. of America. 1957. Price $10.00.

Vertebrates of the United States by W. F. BLAIR, A. P. BLAIR, P. BRODKORB, F. R. CAGLE & G. A. MOORE. New York: McGraw Hill. 1957. Price $12.00.

Diseases of Pigs by H. I. FIELD. London: H.M.S.O. (M.A.F.F. Bulletin No. 171). 1957. Price 3*s*. 6*d*.

A Handbook of Animal Physiology by E. M. PANTELOURIS. London: Baillière, Tindall & Cox. 1957. Price 25*s*.

Annales Instituti Biologici (Tihany) Hungaricae Academiae Scientiarum. Vol. XXIV (for 1955-56). Tihany 1957.

International Union for the Conservation of Nature and Natural Resources. Proceedings of the Sixth Technical Meeting, Edinburgh, June 1956. London: S.P.N.R. 1957. Price 25*s*.

The Wildfowl Trust—Eighth Annual Report (for 1954-56) edited by P. SCOTT & H. BOYD. London: Country Life. 1957. Price 10*s*.

Proceedings of the New Zealand Ecological Society. No. III March 1956 (price 3*s*.); No. IV May 1957 (price 7*s*. 6*d*.). Wellington: N.Z. Ecol. Soc. (P.O.B. 202).

ABSTRACTS

The abstracts are edited by Professor L. A. Harvey with the assistance in selecting and abstracting of J. A. Allen, J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, P. D. Gabbutt, N. A. Holme, S. J. Holt, D. Leatherdale, A. Macfadyen, J. M. D. Mackenzie, C. Matheson, E. J. Moynahan, Miss E. M. Nelmes, W. R. Pickering, D. Scott, J. L. Cloudsley-Thompson, G. G. Vickers, Mrs M. Vincent, M. Williamson and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, The University, Exeter.**

Separate copies of the abstracts suitable for mounting on cards can be obtained from **Blackwell Scientific Publications Ltd., 24-25 Broad Street, Oxford,** or through any bookseller; price 5*s.* 6*d.* per annum, post free (issued in May and November). Back numbers of the 'Notices of publications ...' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s.* for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Arnold, D. C. (1957). The response of the limpet, *Patella vulgata* L., to waters of different salinities. *J. Mar. Biol. Ass. U.K.* **36,** 121-8.
The effect of splashing limpets with water of varying salinity.

Baird, R. H. & Gibson, F. A. (1956). Underwater observations on escallop (*Pecten maximus* L.) beds. *J. Mar. Biol. Ass. U.K.* **35,** 555-62.
The behaviour, distribution and biology of the escallop on Irish beds, studied with the aid of self-contained diving apparatus.

Barnes, H. (1957). The northern limits of *Balanus balanoides* (L.). *Oikos,* **8,** 1-15.
The northern limits of this and other barnacles, and also some littoral molluscs, may be correlated with the summer limits of the ice pack, the effect of the latter being indirect through severity of conditions and the time available for nauplius release and settlement.

Blacker, R. W. (1957). Benthic animals as indicators of hydrographic conditions and climatic change in Svalbard waters. *Fish. Invest. Lond.* (2), **20,** (10), 1-49.
An historical account of work off Spitzbergen and Bear Island since 1878 and discussion of recent sampling by the *Ernest Holt*. Charts the distribution of selected species relating it to temperature, depth and mode of reproduction. Uses indicator species (described in an appendix) to demonstrate hydrographic changes resulting largely from a greater influx of Atlantic water.

Bowers, A. B. (1956). Age and size of manx herring in 1955. *Rep. Mar. Biol. Sta. Pt Erin,* **68** (1955), 17-19.

Bowers, A. B. (1957). Age and size of manx herring in 1956. *Rep. Mar. Biol. Sta. Pt Erin,* **69** (1956), 18-20.

Buchanan, J. B. (1957). Benthic fauna of the continental edge off Accra, Ghana. *Nature, Lond.* **179,** 634.
Almost the entire assemblage Mediterranean in character. There is possibly a direct continuity of marine benthic forms from Morocco to the Gulf of Guinea, due to the peculiar temperature conditions of coastal waters off West Africa.

Crisp, D. J. (1957). Effect of low temperature on the breeding of marine animals. *Nature, Lond.* **179,** 1138-9.
Two arctic barnacles *Balanus balanoides* and *B. balanus* are normally fertilized once a year. Kept at between 14° and 18° C over long periods no copulation or fertilization occurred. Barnacles brought a few days before normal breeding season bred under these conditions. Kept at 3°-10° C breeding occurs out of season.

Cushing, D. H. (1957). The number of pilchards in the Channel. *Fish. Invest. Lond.* (2), **21,** (5), 1-27.
Uses quantitative samples of eggs, larvae, phyto- and zoo-plankton and echo traces of shoals and landing records to provide estimates of the population of adult fish and their vertical and horizontal movements. Estimates correlation of temperature and spawning and relations between fish, spawn and plankton.

Galliford, A. L. [1956]. Notes on the ecology of pools in the salt marshes of the Dee estuary. *Proc. Liverpool Nat. Fld. Cl.* **1955,** 15-19.
A description of the pools with the range of salinity and temperature on various dates; also a list of the Rotifera found, with dates, salinity and temperature range.

Green, J. (1957). The growth of *Scrobicularia plana* (da Costa) in the Gwendraeth estuary. *J. Mar. Biol. Ass. U.K.* **36,** 41-7.
Population study of a mud flat lamellibranch.

Hepper, B. T. (1957). Notes on *Mytilus galloprovincialis* Lamarck in Great Britain. *J. Mar. Biol. Ass. U.K.* **36,** 33-40.
The detailed distribution, systematics and resistance to *Mytilicola* infection of the Mediterranean mussel.

Mistakidis, M. N. (1957). The biology of *Pandalus montagui* Leach. *Fish. Invest. Lond.* (2) **21** (4), 1-52.
Analyses the life history of the 'pink shrimp' from examination of 25 000 animals from the Thames area. Data on breeding season, egg production, sex reversal, growth rate, length of life, gregarious habits and migrations. Food mostly polychaetes, nearly half of which are *Sabellaria spinulosa*. The only parasite found was the bopyrid *Hemiarthrus abdominalis*.

Morton, J. E. (1956). The tidal rhythm and action of the digestive system of the lamellibranch *Lasaea rubra*. *J. Mar. Biol. Ass. U.K.* **35,** 563-586.
The effect of tidal periodicity on the digestion in the minute lamellibranch *Lasaea rubra* is shown by variations in the processes of digestion and absorption in populations from different tidal levels. Digestion may be both intracellular and extracellular.

Ranade, M. R. (1957). Observations on the resistance of *Tigriopus fulvus* (Fischer) to changes in temperature and salinity. *J. Mar. Biol. Ass. U.K.* **36,** 115-119.
The salinity and temperature tolerances of a common tide pool copepod.

Slinn, D. J. (1956). Phosphate and oxygen in sea water off the Isle of Man during the years 1952-54. *Rep. Mar. Biol. Sta. Pt Erin.* **68** (1955), 30-38.
Owing to mixing, doubtful whether phosphate is ever a limiting factor in phytoplankton production off Port Erin and to the west of the Isle of Man.

Slinn, D. J. (1957). Phosphate and oxygen in sea water off Port Erin during the years 1955 and 1956. *Rep. Mar. Biol. Sta. Pt Erin,* **69** (1956), 29-33.

Smith, W. C. (1957). Gonad condition, age and size of manx herrings, 1945-53, and comparison with earlier years. *Rep. Mar. Biol. Sta. Pt Erin,* **69** (1956), 21-28.

Southward, A. J. (1956). The population balance between limpets and seaweeds on wave-beaten rocky shores. *Rep. Mar. Biol. Sta. Pt Erin,* **68** (1955), 20-29.
On such shores the population of algae, limpets and possibly barnacles are dynamically related, the proportion of algae at any one time depending on the position of the equilibrium between the animals. Any change in this balance may cause cyclic fluctuations lasting upwards of five years and thus prevents exact comparison of intertidal zonation at different places at the same time.

Southward, E. C. (1957). The distribution of Polychaeta in offshore deposits in the Irish Sea. *J. Mar. Biol. Ass. U.K.* **36,** 49-75.
The distribution of the polychaete population taken by good sampling in various grounds south of the Isle of Man.

Williamson, D. I. (1956). Planktonic evidence for irregular flow through the Irish Sea and North Channel in the autumn of 1954. *J. Mar. Biol. Ass. U.K.* **35,** 461-466.
The distribution of *Biddulphia sinensis, Sagitta setosa* and *Isias clavipes* in late September and early October 1954 suggest that the flow through the Irish Sea and North Channel was intermittent at that period.

(*b*) Fresh Water

Becker, P. (1957). Changes in response to light stimuli of the larvae of *Culicoides circumscriptus*. *Nature, Lond.* **180,** 559-560.
Behaviour with respect to light varies with hunger. This is useful in determining types of material on which larvae feed.

Cocking, A. W. (1957). Relation between the ultimate upper lethal temperature and the temperature-range for good health in the roach (*Rutilus rutilus*). *Nature, Lond.* **180,** 661-662.

Roach maintain condition at 26° C, die after a few weeks at 30° C and die within a week at 32° C. A gradual rise in temperature has deleterious effects above 30° C. The ultimate upper lethal temperature has little relation with range for health and breeding, and fish may disappear from water below the u.l.t. Criteria are suggested by which the thermal relationships may be compared.

Edwards, R. W. (1957). Vernal sloughing of sludge deposits in a sewage effluent channel. *Nature, Lond.* **180,** 100.

This is associated with the emergence of chironomids. The sudden release of organic material into the water is likely to reduce the oxygen concentration, and promote other conditions adverse to fish.

Hanna, H. M. (1957). Observations on case-building by the larvae of *Limnephilus politus* McLachlan and *L. marmoratus* Curtis (Trichoptera: Limnephilidae). *Proc. R. Ent. Soc. Lond.* (A), **32,** 47-52.

The case of *L. politus* is started by the construction of a belt; that of *L. marmoratus* by a ventral plate and square. The growth of the case parallels that of the larva and increase in size is achieved by adding to the anterior end and cutting away from the posterior end.

Macan, T. T. (1957). The life histories and migrations of the Ephemeroptera in a stony stream. *Trans. Soc. Brit. Ent.* **12,** (5), 129-156.

Monthly collections were made over a period of three years from a stream in the Lake District, and the life histories of seven species studied. Of these, only *Ephemerella ignita* is a true summer species passing the rest of the year as dormant eggs: the remainder grow in autumn and spring. Variations in life histories from place to place are ultimately due to high summer temperatures and possibly oxygen deficiency.

Rapoport, E. H. (1957). Population studies on three species of Cladocera. *Nature, Lond.* **179,** 637.

In *Bosmina obtusirostris* there is relation between season and the proportion of females bearing eggs. The species is very variable in the composition of the population. In *Moina micrura* there is uniformity in the composition of the population in successive samples. *Moina eugeniae* replaced *M. micrura* in June 1951 in one lagoon.

(*c*) Land

Albrecht, F. O. & Blackith, R. E. (1957). Phase and moulting polymorphism in locusts. *Evolution,* **11,** 166-177.

Demonstrates developmental polymorphs in red and desert locusts characterized by size and growth rate differences and numbers of moults. Discusses the phenomena and their significance in the ecology of the animals.

Allen, A. A. (1957). The habit of aggregation in *Agonum dorsale* Pont. (Col., Carabidae). *Ent. Mon. Mag.* **93,** 142.

A very large aggregation of the beetle *Agonum dorsale* is recorded under a dustbin lid.

Ash, J. S. (1957). Post-mortem examinations of birds found dead during the cold spells of 1954 and 1956. *Bird Study,* **4,** 159-166.

Records of body weight, disease and parasites from nine casualties in 1954 and twenty-nine in 1956. Discusses probable causes of death.

Barlee, J. (1957). The soaring of gannets and other birds in standing waves. *Ibis,* **99,** 686-687.

Waves formed by strong winds to leeward of islands are used by gannets, herring gulls and fulmars for soaring, and by gannets coming in low against the wind at Bass Rock to rise before gliding to their nests. Rooks also use standing waves to gain height.

Blackith, R. E. (**1957**). Polymorphism in some Australian locusts and grasshoppers. *Biometrics*, **13**, 183-196.
Uses dispersion matrices to construct three-dimensional generalized distance charts of various forms of polymorphism in orthopterans.

Boyd, A. W. (**1957**). Sewage-farms as bird-habitats. *Brit. Birds*, **50**, 253-263.
Ecological notes on the various habitats afforded by sewage-farms, and on the preferences shown by different species. [Includes a section on Nottingham Sewage Farm by Dr R. J. Raines.]

Boyd, H. (**1957**). Early sexual maturity of a female mallard. *Brit. Birds*, **50**, 302-303.
A marked female mallard known to be scarcely six months old was with four ducklings in early November. It is possible the rather frequent late autumn broods of mallard may be produced by early-maturing females.

Boyd, H. (**1957**). Mortality and kill amongst British-ringed teal *Anas crecca*. *Ibis*, **99**, 157-177.
An analysis of returns from the ringing of 11 506 teal between 1945 and 1955. Man is responsible for nearly 92% of reported deaths, but the true proportion is probably about three-fifths for males and one-half for females. About two-thirds of the male and more than half the female casualties occur between September and March.

Boyd, H. (**1957**). Mortality and fertility of the white-fronted goose. *Bird Study*, **4**, 80-93.
Estimates breeding success and incidence of mortality at different stages in the life history of the bird. Concludes that the population is stationary, fecundity being apparently adapted in relation to the prevalence of large-scale breeding failures.

Boyd, H. J. (**1957**). Results of ringing guillemots and razorbills on Lundy, 1947-56. *Rep. Lundy Fld. Soc.* **1956**, 19-25.
A statistical paper, which confirms the results of Thomson (1953, *Brit. Birds*, **46**, 3-15) for the auk populations of south-west England and South Wales. The population is decreasing and undue mortality among adults is indicated.

Briggs, J. B. (**1957**). Some experiments on control of ground beetle damage to strawberry. *Rep. E. Malling Res. Sta.* A **40** (1956), 142-145.
The type of damage caused to strawberries by different species of ground beetle is described. No safe chemical control can be recommended as yet; suggestions for such control are made.

Brindle, A. (**1957**). The effect of temperature and humidity on the flight of Trichoptera. *Ent. Mon. Mag.* **93**, 63-66.
Field observations suggest that high temperature and high humidity are both favourable to day and night activity of adult caddis flies (Trichoptera). It is considered that wind may control the direction of flight.

Campbell, B. (**1955**). The breeding distribution and habits of the pied flycatcher (*Muscicapa hypoleuca*) in Britain. Part 3: Discussion. *Bird Study*, **2**, 179-191.
Analyses the habitat of the bird, in open deciduous woods on the foothills of highland Britain, in relation to the needs for food supply on arrival, cover, nest-sites, song perches, nest materials and food for adults and young. Discusses the importance of nest boxes for the species and analyses ecological distribution in Britain.

Carnegie, A. J. M. (**1956**). The effects of varying temperatures on the rate of emergence of adult male mussel scale (*Lepidosaphes beckii* Newm.) (Hem., Coccidae). *Ent. Mon. Mag.* **92**, 311-312.
Laboratory and field observations showed that most adult males emerged during a rise of temperature.

Chitty, H. & Austin, C. R. (1957). Environmental modification of oestrus in the vole. *Nature, Lond.* **179,** 592-593.

Experimental evidence for the occurrence of two kinds of oestrus behaviour. A short cycle, with a brief receptive period, and a prolonged oestrus state, coitus being associated with induced ovulation. Environmental conditions, such as social stress, may be a decisive factor.

Clarke, K. U. (1957). On the increase in linear size during growth in *Locusta migratoria* L. *Proc. R. Ent. Soc. Lond.* (A), **32,** 35-39.

Linear size increases during a stadium, as well as at ecdysis, providing the structure measured contains both sclerites and intersegmental tissue. This does not reflect true growth. The folding of the intersegmental membranes, beneath the sclerites and their unfolding during each stadium brings about the increase in linear measurement observed. The sclerotic plates increase in their dimensions only at ecdysis. The dominant type of growth shown by the whole animal is related to the proportion of sclerotic plate/intersegmental membrane in the exoskeleton.

Coulson, J. C. & White, E. (1957). Mortality rates of the shag estimated by two independent methods. *Bird Study,* **4,** 166-171.

An estimate of 44% mortality from recoveries of dead shags is regarded as excessive owing to ring losses. Estimates by Jackson's 'negative method' on the Farne Islands gave a figure of 14%.

Cullen, E. (1957). Adaptations in the kittiwake to cliff-nesting. *Ibis,* **99,** 275-302.

The breeding behaviour of the kittiwake *Rissa tridactyla* was studied during three seasons on the Farne Islands, and the patterns of its activities are compared with corresponding activities of ground-nesting gulls. Other adaptations are: the normal clutch is two instead of three, the young are not cryptic, and the claws and toe muscles are more strongly developed.

Davis, P. (1957). The breeding of the storm petrel. *Brit. Birds,* **50,** 85-101, 371-384.

A detailed study of the breeding biology of the storm petrel *Hydrobates pelagicus,* the result of three seasons' observations at Skokholm, Pembrokeshire, of marked birds in burrows adapted for daily inspection. During the second summer a simple method of sexing the adults was found. Of 37 chicks hatched 32 reached the fledgling stage.

Deans, A. S. C. (1957). Honey from heather. *Agriculture,* **64,** 63-69.

Honey from ling is highly valued for its unique flavour, but production involves a special technique in bringing the foraging bees to selected moorland sites.

Donald L. G. (1957). Ragwort poisoning. *Agriculture,* **64,** 131-133.

Ragwort continues to spread and more cases of poisoning occur every year, particularly in cattle, than is generally recognized.

Dowdeswell, W. H., Ford, E. B. & McWhirter, K. G. (1957). Further studies on isolation in the butterfly *Maniola jurtina* L. *Heredity,* **11,** 51-65.

A further contribution on the spot patterning of this butterfly on the Scilly Isles.

Gabbutt, P. D. (1956). The spiders of an oak wood in south-east Devon. *Ent. Mon. Mag.* **92,** 351-358.

Samples were taken from the litter of an oak wood and the spiders collected. The seasonal variations and variations between stations are discussed.

Georgala, M. B. (1957). A contribution to the biology of the pear sucker, *Psylla pyricola* Föer. *Rep. E. Malling Res. Sta.* (A) **40** (1956), 135-141.

Techniques for hatching and rearing the pear sucker through five nymphal instars in the laboratory are described. In the field three generations occurred in south-east England in 1955. It was possible to distinguish the population peaks of the two pale summer generations, in spite of overlapping. The third generation was dark and overwintered mainly among the spur growth of pear trees.

Gradwell G. R. (1957). Habits of larvae of *Malachius bipustulatus* (L.) (Col., Malachidae). *Ent. Mon. Mag.* **93,** 104.

The numbers of larvae of the beetle *Malachius bipustulatus* ascending trees during winter are recorded, and it was noted that there was a drop over the winter. It is considered that eggs are laid and pupation takes place in the soil.

Groves, E. W. (1957). Material used in a long-tailed tit's nest on Bookham Common, Surrey. *Lond. Nat.* **36** (1956), 57-58.

Hayward, J. F. (1956). A preliminary note on Pleistocene plant galls from the Lea valley and elsewhere. *Ent. Mon. Mag.* **92,** 301-303.

Fossil galls are described from the oaks *Quercus robur* and *Q. petraea* and the galling organism indicated. The possibility of a gall on seeds of iris, *Iris pseudacorus,* is discussed.

Henson, W. R. (1957). Temperature preference of *Grylloblatta campodeiformis* (Walker). *Nature, Lond.* **179,** 637.

These orthopteran insects only enter the air when it is saturated, they are negatively phototactic, and show a low-temperature preference. The insect moves deeper into the soil at times of surface heating and cooling. This may explain the apparent seasonal differences in abundance.

Howe, R. W. (1956). Studies on beetles of the family Ptinidae. 14. The biology of *Ptinus pusillus* Sturm. *Ent. Mon. Mag.* **92,** 331-333.

Notes are given on the effects of temperature on the life cycle in the laboratory.

Howe, R. W. (1956). Studies on beetles of the family Ptinidae. 15. The biology of *Ptinus hirtellus* Sturm and some notes on *P. latro* F. *Ent. Mon. Mag.* **92,** 369-372.

Cultures of *Ptinus hirtellus* were kept in controlled laboratory conditions and the duration of various stages in the life history is given for different temperatures and humidities. Similar notes are given for *P. latro.*

Jenkins, D. (1957). The breeding of the red-legged partridge. *Bird Study,* **4,** 97-100.

Data on clutch size, polyandry and social behaviour in broods derived from marked birds.

Kettle, D. S. (1957). Preliminary observations on weather conditions and the activity of biting flies. *Proc. R. Ent. Soc. Lond.* (A) **32,** 13-20.

The results of a 24-hour study of weather conditions and the biting and flying activity of biting flies. High light intensity and warmth in relation to the activity of *Haematopota pluvialis* and *H. crassicornis* and low light intensity and calm conditions in the case of *Culicoides impunctatus* are thought to be of prime importance.

Lack, D. (1956). Further notes on the breeding biology of the swift. *Ibis,* **98,** 606-619.

The influence of weather on breeding success is such that broods of three are reared normally in fine summers only, of two in all but very wet summers, and of one every year. In wet summers nestling periods are longer and weights are lower.

Lack, D. (1957). Notes on nesting nightjars. *Brit. Birds,* **50,** 273-277.

Observations in Suffolk made in late June and early July 1952-1956. Eggs of the second brood were normally laid within two days of the male attending the first brood by day. Chicks increase steadily in weight, and do not decrease in bad weather.

Locket, G. H. & Marsh, M. D. (1957). Two cases of Lycosid spiders carrying snail eggs instead of egg cocoons. *Ent. Mon. Mag.* **93,** 139.

Lycosa tarsalis and *L. purbeckensis* are recorded as carrying snail shells of approximately the same size as their egg cocoons on their spinnerets.

London Natural History Society (1957). The survey of Bookham Common. Fifteenth Year. *Lond. Nat.* **36** (1956), 50-58.

Progress report including changes in bird population, gall midges, Lepidoptera and materials used in a long-tailed tit's nest.

Mackenzie, J. M. D. (1956). Effect of myxomatosis on tit nests. *Scot. Nat.* **68,** 119-120.
The disappearance of rabbits necessitated substitutes for their fur in the nest material of great, blue and coal tits.

Maelzer, D. A. (1956). Value of pF scale for water in an ecological study of an insect living in soil. *Nature, Lond.* **178,** 874.
The scale measures energy with which water is held in soil. The ovipositional response of the cockchafer *Aphodius howitti* appears to be a function of the force holding the water rather than the water content of the soil. The optimum range was about 2·8, irrespective of soil type. This is important in understanding the distribution and abundance of the species in South Australia.

Marler, P. R. (1956). Evolution of finch colours. *Middle-Thames Nat.* **8** (1955), 4-6.
In finches, conspicuousness of coloration is inversely related to palatability, and the position of conspicuous markings in different species is related to the different attitudes and movements adopted during threat displays.

Marshall, A. J. & Disney, H. J. de S. (1957). Experimental induction of the breeding season in a xerophilous bird. *Nature, Lond.* **180,** 647-649.
Quelea quelea has an innate urge to build nests. For successful nest building long green grass is necessary. The internal rhythm can be modified by external conditions, including possibly rainfall and social stimulation.

Meinertzhagen, R. (1957). Bird semantics as an aid to avian systematics. *Ibis,* **99,** 346-347.
Suggests that prolonged isolation results in changes in the notes of a species sufficient to discourage pairing when two races come together again as in the *Larus argentatus - fuscus* group of gulls.

Middleton, A. D. (1957). Game birds on the farm—1. *Agriculture,* **64,** 270-273.
Game birds are a valuable biproduct of farming. Nesting cover and feeding are discussed.

Middleton, A. D. (1957). Game birds on the farm—2. *Agriculture,* **64,** 345-347.
Protection against nesting hazards and conservation of breeding stock are necessary for a profitable return.

Mitchell, K. D. G. (1957). Further aircraft observations of birds in flight. *Brit. Birds,* **50,** 291-302.
Observations show similarities to a previous series (see Mitchell, K. D. G., 1955, *Brit. Birds,* **48,** 59-70. Abstract in 1956, *J. Anim. Ecol.* **25,** 208).

Moore, N. W. (1957). Territory in dragonflies and birds. *Bird Study,* **4,** 125-130.
Discusses primarily territorial behaviour among dragonflies, contrasting this and its effects with that of birds.

Moore, N. W. (1957). The past and present status of the buzzard in the British Isles. *Brit. Birds,* **50,** 173-197.
A summary of the buzzard's past status and of the results of a survey made in 1954. The ecological status and causes of population changes during the past 150 years are discussed.

Nicholson, E. M. and others (1957). The rarer birds of prey: their present status in the British Isles. *Brit. Birds,* **50,** 129-155.
The present populations of golden eagle, goshawk, kite, honey buzzard, marsh harrier, hen harrier, Montagu's harrier, osprey, hobby and peregrine are estimated, their regional distributions given, and fluctuations are shown to depend on whether or not they suffer from human disturbance.

O'Ruadhain, M. (1956). The position of nature protection in Ireland in 1956. *Irish Nat. J.* **12,** 81-104.
A useful summary of measures for wild life protection, including reserves, in Eire.

Pearce, E. J. (**1957**). The resistance of the Pselaphidae (Col.), etc., to low temperatures. *Ent. Mon. Mag.* **93,** 104.

Various arthropods were subjected to temperatures of 24°-25° F for several days. The Pselaphidae showed better resistance to their conditions than some other insects, spiders and isopods.

Sankey, J. H. P. (**1956**). Behaviour of pupae of *Celerio euphorbiae* (L.) (Lep., Sphingidae). *Ent. Mon. Mag.* **92,** 333.

Pupae removed from cocoons and placed on sand ventral face down were found subsequently to have turned ventral face upwards.

Schreider, E. (**1957**). Ecological rules and body-heat in man. *Nature, Lond.* **179,** 915-916.

Two clines for body weight to surface area ratio, in black and in white racial groups. Limb length to body weight ratio also shows a general geographical gradient following Allen's rule. More samples may reveal two or more distinct clines. Experiments show a significant relation between body temperature and the ratios mentioned.

Scott, H. (**1957**). Recent studies of the life-history of cave beetles of the genus *Speonomus* (Silphidae, Bathysciinae). *Ent. Mon. Mag.* **93,** 32-34.

In the cavernicolous Silphid beetle *Speonomus longicornis* a single large egg is laid at a time. The larva after a brief period of activity constructs a small cell in which it remains in a state of diapause until pupation takes place. Notes are given on a similar species *S. delarouzeei*.

Scott, P. (**1956**). A population study of the pink-footed goose.

Boyd, H. (**1956**). Calculating methods used in the study. *Proc. Linn. Soc. Lond.* **166,** 15-16.

A joint abstract of the two papers. The colony at Hofsjökull Ice-cap, Iceland, had about 8600 adults and 10 900 goslings in 1953. The British wintering population was of the order of 36 000-41 000 in the early autumn of 1952 and 1953. About 26% of adults die annually.

Skutch, A. F. (**1957**). The incubation patterns of birds. *Ibis,* **99,** 69-93.

Classifies the known methods of incubation of the birds of the world on the part taken by the sexes.

Southgate, B. J. (**1957**). Windsor nature reserve. *Middle-Thames Nat.* **9,** 10-14.

A short account, mainly historical, of the Windsor Forest National Nature Reserve, Berkshire.

Southwood, T. R. E. (**1957**). Observations on swarming in Braconidae (Hymenoptera) and Coniopterygidae (Neuroptera). *Proc. R. Ent. Soc. Lond.* (A) **32,** 80-82.

Describes swarming in *Blacus ruficornis* and *Coniopteryx tineiformis*.

Steven, D. M. (**1957**). The bank vole in captivity. *Nature, Lond.* **179,** 33-34.

Discusses seasonal breeding, and variation in gestation period. Some evidence of winter breeding, the latter being less seasonal than thought. Gestation period at least as variable as in humans.

Tew, R. P. & Groves, J. R. (**1957**). Some observations on the effects of formulation on the persistence of DDT and its toxicity to certain orchard insects and mites. *Rep. E. Malling Res. Sta.* (A) **40** (1956), 152-160.

It was found that DDT sprayed in emulsions persisted longer than suspensions. The significant increase in phyllophagous mite populations is shown to be due to the application of DDT. Low populations and great variability prevented the assessment of the effects of the different formulations on the codling moth *Ernarmonia pomonella*. DDT had a pronounced contact toxicity on typhlodromid mites.

Varley, G. C. (1957). Attitudes of the larva of the lobster moth, *Stauropus fagi* (L.) (Lep., Notodontidae). *Ent. Mon. Mag.* **93,** 92-94.

The various attitudes adopted by the larva of the lobster moth *Stauropus fagi* are described and figured and their significance for larval life discussed.

Wallace, M. M. H. (1957). Field evidence of a density-governing reaction in *Sminthurus viridis* (L.). *Nature. Lond.* **180,** 388-390.

Distribution and abundance of the lucerne flea (Collembola) related to temperature and humidity. But in local populations changes in density occur which are not related to these, and there is evidence that such changes are due to some factor influenced by population density itself. This being a tardy density-governing reaction (Nicholson 1954).

Whalley, P. E. S. (1957). Cocoon formation in two species of weevil (Col., Curculionidae). *Ent. Mon. Mag.* **93,** 96.

Although the banana weevil, *Cosmopolites sordidus* does not normally form a cocoon at pupation, two specimens are recorded which did so. Another weevil, *Temnoschoita nigroplagiata*, always constructs a cocoon.

Williamson, M. H. (1957). Gene and chromosome frequencies in *Peronea comariana* Zell. (Lep., Tortricidae). *Ent. Mon. Mag.* **93,** 52-53.

The genetics of the colour varieties of the Strawberry button moth, *Peronea comariana*, is discussed, and it is concluded that the most recessive alleles are the commonest, and that there is interaction between two recessive alleles.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Allen, P. (1957). Studies of some intercastes of *Myrmica rubra* L. (Hym., Formicidae). *Ent. Mon. Mag.* **93,** 136-139.

Descriptions are given of intercaste material of *Myrmica rubra* and correlation of certain morphological characters in this material is demonstrated.

Allen, P. (1957). The larval morphology of Agromyzidae (Diptera). *Proc. R. Ent. Soc. Lond.* (A) **32,** 59-66.

Includes a key to separate some Agromyzidae collected from Umbelliferae using only larval characters.

Andrew, R. J. (1957). A comparative study of the calls of *Emberiza* spp. (buntings). *Ibis,* **99,** 27-42.

Use of the sound spectograph enables comparison of the structure of bunting calls. Homologies between the calls of ten different species are established and their probable evolution traced.

Baker, C. S. Wood (1957). The winged viviparous female of *Vesiculaphis theobaldi* Tak. (syn. *Trilobaphis caricis* Theo.) (Hem., Aphididae). *Ent. Mon. Mag.* **93,** 82-84.

A description is given of the winged viviparous females of the aphid *Vesiculaphis theobaldi*, and notes are given on food plants and behaviour.

Barfoot, S. D. (1957). *Phania vittata* Meig., a Tachinid fly new to Britain. *Ent. Mon. Mag.* **93,** 85.

A description is given of a Tachinid male, *Phania vittata*, as being new to Britain.

Bowers, A. B. (1957). Nature of the spawning area in herrings. *Nature, Lond.* **179,** 926.

Points out that herring spawn has been taken by dredge, grab and a modified tow netting technique. See 1957, *Nature,* **179,** 638.

Briggs, J. B. (1956). Notes on the biology and identification of some allies of the winter moth (*Operophtera brumata* (L.)). *Rep. E. Malling Res. Sta.* A **39** (1955), 141-145.
Some features of use in the identification of certain allies of the winter moth on fruit trees are described, with keys to apterous females and larvae. Biological notes are given for the more important species.

Brindle, A. (1957). Notes on the use of light for attracting Trichoptera. *Ent. Mon. Mag.* **93,** 127-129.
The use of Tilley lamps for trapping nocturnal adult Trichoptera is discussed. The short-range attraction of the lamp is emphasized, and the siting considered in relation to the behaviour of the adults.

Bryce, D. (1957). Notes on the life histories of British Limoniinae (Dipt., Tipulidae). 1. *Limonia nubeculosa* Meig., and *L. didyma* Meig. *Ent. Mon. Mag.* **93,** 67-69.
Descriptions are given of the crane-fly larvae *Limonia nubeculosa* and *L. didyma.*

Bryce, D. (1957). Notes on the life histories of British Limoniinae (Dipt., Tipulidae). 2. *Ula sylvatica* Meigen. *Ent. Mon. Mag.* **93,** 132.
Ula sylvatica, which does not appear to have been fully described in the larval stage, is briefly described and figured.

Burges, H. D. (1957). Studies on the Dermestid beetle *Trogoderma granarium* Everts. 1. Identification and duration of the developmental stages. *Ent. Mon. Mag.* **93,** 105-110.
The Khapra beetle *Trogoderma granarium* was bred at 30° C and 70% R.H. from eggs and the external morphology of the larval instars studied. Data are given for the duration of the various stages, and notes are given for the separation of the instars.

Collyer, E. & Groves, J. R. (1956). Some tetranychid mites on fruit trees. *Rep. E. Malling Res. Sta.* A **39** (1955), 135-138.
Four species of tetranychid mites found on fruit trees in Kent and Essex are described. A key for separating six species of tetranychid mites is included.

Currie, R. I. & Foxton, P. (1957). A new quantitative plankton net. *J. Mar. Biol. Ass. U.K.* **36,** 17-32.
A vertical closing plankton net equipped with a combined depth recorder and flow meter.

Drinnan, R. E. & Ridpath, M. G. (1957). Counting flocks of roosting birds by photography. *Bird Study,* **4,** 149-159.
Discusses difficulties of visual counting of large flocks and describes critically methods using both still and ciné photography.

Edwards, V. C. Wynne- (1957). The so-called 'northern golden plover'. *Scot. Nat.* **69,** 89-93.
Breeding populations of *Charadrius apricarius* in the British Isles, the Faeroes and Iceland all contain varying proportions of the plumage types named *apricarius* and *altifrons* with many intermediates. It is suggested that trinomial names should no longer be used, at least for birds seen in the British Isles.

Emlen, J. T., Jr. (1956). A method for describing and comparing avian habitats. *Ibis,* **98,** 565-576.
A scheme of habitat description based on the selection of measurable features. Examples show how quantitative habitat data can be applied in making semi-pictorial diagrams and in analysing subtle differences of habitat selection.

Gradwell, G. R. (1957). A new tetrastichine (Hym., Eulophidae) genus with three included species. *Ent. Mon. Mag.* **93,** 1-5.
A genus *Pronotalia* gen. nov. is described containing three species *Pronotalia trypetae* sp.n., *P. liparae* sp.n., and *P. valkeilai* sp.n.

Graham, M. W. R. de V. (1956). A new genus and species of Pteromalidae (Hym., Chalcidoidea). *Ent. Mon. Mag.* **92,** 406-408.

A female chalcidoid wasp is described as belonging to a new genus and species, *Mesopilon exiguum* sp.n.

Le Quesne, W. J. (1956). An examination of the British species of *Drymus* Fieber (Hem., Lygaeidae) with a new subgenus and an addition and a generic reassignment in the British list. *Ent. Mon. Mag.* **92,** 337-341.

A new subgenus *Sylvadrymus* is erected within *Drymus* and a key to the species of *Drymus* is given.

Le Quesne, W. J. (1957). A practical key to the British genera of Rhyparochrominae (Hem., Lygaeidae), including some generic reassignments. *Ent. Mon. Mag.* **93,** 57-62.

Of the four British species regarded as belonging to the genus *Rhyparochromus*, three are transferred to two other genera. A key is given to the genera of Rhyparochrominae.

Leston, D. (1957). The British *Lygocoris* Reuter (Hem.: Miridae) including a new species. *Entomologist,* **90,** 128-135.

Includes a key to the six British species. The new one here described is *L. populi,* from species of *Populus* in southern England.

MacDowall, J. (1957). Soil thermometers. *Nature, Lond.* **179,** 328.

Errors disappeared when a microcrystalline wax was used as lagging in place of paraffin wax.

Mackenzie, J. M. D. (1957). Crested tits in plantations. *Scot. Nat.* **69,** 58-59.

Artificial calling as a rough method of assembling birds and counting them.

Pearce, E. J. (1957). *Cephennium gallicum* Ganglbaur (Col., Scydmaenidae) the common British *Cephennium,* and not *C. thoracicum* (Mueller and Kunze). *Ent. Mon. Mag.* **93,** 135.

It is pointed out that *Cephennium thoracicum* has not been recorded for Britain and distinguishing points between the two species are given.

Pitcher, R. S. (1956). A further note on the cambium miner of *Prunus* spp. (*Dendromyza cerasiferae* Kangas, Agromyzidae, Dipt.). *Rep. E. Malling Res. Sta.* A **39** (1955), 139-140.

An account is given of all stages of the life history of the cambium miner of *Prunus* spp., *Dendromyza cerasiferae.* Reference is also made to parasitism and economic importance.

Reid, E. T. M. (1957). The diagnostic value of the foretarsus in male anopheline mosquitoes (Dipt., Culicidae). *Ent. Mon. Mag.* **93,** 7-10.

The size and shape of the foretarsus was examined in fourteen species of Ethiopian mosquitoes. It was considered that the shape and size of the tarsal claw and last tarsal segment were of limited taxonomic use.

Scudder, G. G. E. (1957). A new genus and species of Rhyparochrominae (Hem., Lygaeidae). *Ent. Mon. Mag.* **93,** 143-144.

Dilompus robustus, a new genus and species is described.

Slack, F. E. (1956). A key to the British species of the genus *Cyclops* O. F. Muller. *Glasgow Nat.* **17,** 250-256.

A key to forty-five species of these freshwater copepods.

Smith, K. G. V. (1956). Notes on the immature stages of four British species of *Lonchaea* Fln. (Dipt., Lonchaeidae). *Ent. Mon. Mag.* **92,** 402-405.

Diagnostic characters are described and figures are given for the larvae, *Lonchaea flavidipennis, L. deutschi, L. cariecola* and *L. palposa.* Notes are also given for the puparium.

Smith, K. G. V. (1957). Selection of a lectotype of *Tetanocera robusta* Loew (Dipt., Sciomyzidae). *Ent. Mon. Mag.* **93,** 70-71.
Consequent upon confusion between the marsh flies *Tetanocera robusta* and *T. ferruginea*, a lectotype is selected for the former.

Smithers, C. N. (1956). The male of *Ectopsocopis mozambicus* (Badonnel) (Psocoptera, Peripsocidae). *Ent. Mon. Mag.* **92,** 306-307.
A description is given of the hitherto unknown male.

Southwood, T. R. E. & Scudder, G. G. E. (1956). The immature stages of the Hemiptera-Heteroptera associated with the stinging nettle (*Urtica dioica* L.). *Ent. Mon. Mag.* **92,** 313-325.
Descriptions are given of *Heterogaster urticae, Anthocorus nemorum, A. nemoralis, Deraeocoris ruber, Plagiognathus arbustorum, P. chrysanthemi, Orthonotus rufifrons, Orthotylus ochrotrichus, Heterotoma merioptera, Lygus pabulinus, Liocoris tripustulatus, Calocoris sexguttatus, C. alpestris, C. norvegicus*, together with notes on the life cycles. A key to the larvae is given.

Spencer, K. A. (1957). Two new European species of Agromyzidae (Dipt.). *Ent. Mon. Mag.* **93,** 35-36.
Agromyza prespana sp.n. and *Phytagromyza simplonensis* sp.n. are described, and an addition is made to an existing key.

Stelfox, A. W. (1957). Further new species of Dacnusini (Hym., Braconidae) from Ireland and notes on several other species. *Ent. Mon. Mag.* **93,** 111-120.
Descriptions are given of the Braconids, *Gyrocampa ruficollis* sp.n., *G. lanigera* sp.n., *Chorebus hirtigena* sp.n., *C. striola* sp.n., *C. scabrifossa* sp.n., *Chaenusa elongata* sp.n., *C. opaca* sp.n. Notes are also given on other Hymenoptera.

Stroyan, H. L. G. (1956). A note on some aphid material of J. O. Westwood. *Ent. Mon. Mag.* **92,** 381-382.
A discussion is given of the taxonomic categories within the genus *Trama* von Heyden.

Thorpe, W. H. (1957). The identification of Savi's, grasshopper and river warblers by means of song. *Brit. Birds,* **50,** 169-171.
Analyses the songs of three *Locustella* species.

Twinn, D. C. (1956). A method of making permanent mounts of beetle genitalia. *Ent. Mon. Mag.* **92,** 295.
A method is described whereby the genitalia can be easily examined under all powers of magnification, including oil immersion.

Wagner, H. O. (1957). The technical basis of experimental research on bird migration. *Ibis,* **99,** 191-195.
A method using an electro-magnet for measuring the restlessness at night of captive birds is described. Certain factors in the environment are essential. Individuals of the same species vary in their reaction to the same stimuli, and the normal behaviour of the bird under test conditions must be known.

Williams, C. B. & Davies, L. (1957). Simuliidae attracted at night to a trap using ultra-violet light. *Nature, Lond.* **179,** 924-925.
Shows considerable night activity in these Diptera. Location and type of trap, and catches are described. Suction traps show a lower rate of catch.

Woodroffe, G. E. (1957). *Halticus macrocephalus* Fieber (Miridae). An addition to the British list of Hemiptera-Heteroptera. *Entomologist,* **90,** 17-18.
Includes a key for the separation of *H. macrocephalus* (recorded in Cornwall) from the other two British species of *Halticus*.

Woodroffe, G. E. (1957). On the identity of the British *Macrolophus* Fieber (Hem., Miridae), with a key to the European species. *Entomologist*, **90,** 125-127.

M. rubi sp.n. is described from bramble in Britain, where it was formerly confused with *M. nubilis* on *Stachys sylvatica* and was later misidentified as *M. costalis*. Stichel's key to the European species is modified to accommodate it.

3. PARASITES

Barfoot, S. D. (1957). Oviposition of *Ptychomyia selecta* Meig. (Dipt., Tachinidae). *Ent. Mon. Mag.* **93,** 95.

A description is given of females of the Tachinid fly *Ptychomyia selecta* depositing eggs on the sawfly larvae *Nematus ribesii*.

Copland, W. O. (1956). Notes on the food and parasites of pike (*Esox lucius*) in Loch Lomond. *Glasgow Nat.* **17,** 230-235.

Based on the contents of 102 stomachs. Pike were infested with two species of parasitic helminth, the pseudophyllidean cestode *Triaenophorus nodulosus* and the acanthocephalan *Acanthocephalus lucii*.

Crooke, M. (1956). Host of the overwintering generation of *Trichogramma evanescens* Westw. (Hym., Trichogrammatidae). *Ent. Mon. Mag.* **92,** 368.

The pine-looper caterpillar *Bupalus piniarius* is recorded as the host of the overwintering generation of *Trichogramma evanescens*.

Davis, R. A. (1957). Mammal fleas on Skokholm. *Ent. Mon. Mag.* **93,** 25-26.

Three species of fleas, *Hystricopsylla talpae, Ctenopthalmus nobilis vulgaris* and *Nosopsyllus fasciatus*, are recorded from mice on the island.

Gotto, R. V. (1956). The occurrence of a doropygid copepod in a new ascidian host. *Irish Nat. J.* **12,** 110.

Doropygus psyllus on *Ascidia conchilega*.

Gradwell, G. R. (1957). Hosts of three species of *Eulophus* Geoffroy (Hym., Chalcidoidea), one new to science and another new to Britain. *Ent. Mon. Mag.* **93,** 140-142.

Descriptions are given of *Eulophus nigribasis* sp.n., *E. larvarum* and *E. opacula* (Th.), the last being new to Britain. Host records are given.

Michel, J. F. (1957). Husk in adult cattle. *Agriculture*, **64,** 224-228.

Control of the disease must be based on acquired resistance to the lungworm parasite. The ultimate source of infection is the dung of infected animals.

Moir, R. J. & Somers, M. (1956). A factor influencing the protozoal population in sheep. *Nature, Lond.* **178,** 1472.

Concentration of ruminal Protozoa influenced by diet, but other factors may overshadow this. The manner in which the same diet is fed to sheep causes sharp divisions in protozoal counts. Suggests that feeding habits may be an important factor in determination of population level.

Noble, E. R. (1957). Seasonal variations in host-parasite relations between fish and their Protozoa. *J. Mar. Biol. Ass. U.K.* **36,** 143-155.

The variation in protozoan parasite infection of three common marine fish; the intensity of infection may be related to the different feeding habits of the fish.

Slinn, D. J. (1957). *Erpocotyle abbreviata* (Olson, 1876) Price, 1942, a monogenetic trematode new to British waters. *Nature, Lond.* **179,** 271-272.

Three specimens recorded.

Smit, F. G. A. M. (1956). Preliminary descriptions of two new European fleas. *Ent. Mon. Mag.* **92,** 296.

Short descriptions of two new species of fleas, *Ctenophthalmus bisoctodentatus occidentalis* and *Hystrichopsylla talpae orientalis* are given together with remarks on distribution.

Smith, K. G. V. (1957). Some Ichneumonid parasites and a Eulophid hyperparasite (Hym.) bred from egg-sacs of a spider. *Ent. Mon. Mag.* **93,** 102.

Egg sacs of the spider *Tetragnatha extensa* were collected and four genera of Ichneumonid parasites emerged from them. In addition *Pediobius* spp. were recorded as parasitizing cocoons of these Ichneumons.

4. FOOD AND FOOD HABITS

Allen, A. A. (1957). *Tachinus* spp. selected as prey by *Philonthus tenuicornis* M. & R. (Col., Staphylinidae). *Ent. Mon. Mag.* **93,** 94.

In a mixed lot of beetles enclosed in a glass tube, the rove-beetle *Philonthus tenuicornis* attacked and ate species of *Tachinus*.

Birkett, N. L. (1957). Rowan berries attracting moths. *Ent. Rec.* **69,** 75.

Eupsilia transversa and *Conistra vaccinii* congregated in numbers on the berries of rowan at Kendal in October 1953.

Blower, J. G. (1957). Feeding habits of a marine centipede. *Nature, Lond.* **180,** 560.

Scolioplanes maritimus observed feeding at night on *Balanus balanoides* and *Littorina saxatilis*.

Brown, S. C. S. (1957). *Argynnis lathonia* (L.) (Lep., Nymphalidae) attacked by a lizard. *Ent. Mon. Mag.* **93,** 36.

A specimen of the butterfly *Argynnis lathonia* is described in which the wings are thought to have been damaged by a lizard.

Drummond, D. C. (1956). Food plants of *Chrysolina violacea* (Müll.), *C. haemoptera* (L.), *C. crassicornis* (Hell.) and *C. polita* (L.) (Col., Chrysomelidae). *Ent. Mon. Mag.* **92,** 368.

Notes are given on the food plants eaten by the adults or larvae of four species of leaf beetles in the field, and in captivity.

Edwards, R. L. (1956). *Dermestes frischii* Kug. (Col., Dermestidae) attacking the shells of cuttle-fish. *Ent. Mon. Mag.* **92,** 408.

Shipments of cuttle-fish shells were found to contain pupae of the beetle *Dermestes frischii* Kug. It is suggested that the adult beetles lay their eggs on the dead cuttle-fish laid out to dry in the sun, and that the larvae feed on the flesh, subsequently boring into the shell to pupate.

Gibb, J. & Hartley, P. H. T. (1957). Bird foods and feeding-habits as subjects for amateur research. *Brit. Birds,* **50,** 278-291.

Concentration on a single facet of feeding biology is advocated for the amateur. Methods of study and many problems are outlined.

Gradwell, G. F. (1957). A food plant and a parasite of *Athalia cornubiae* Benson (Hym., Tenthredinidae). *Ent. Mon. Mag.* **93,** 12.

The sawfly *Athalia cornubiae* Benson is recorded as feeding on *Sedum album*. The tachinid fly *Meigenia mutabilis* is recorded as a parasite from the larva.

Grensted, L. W. (1956). Ants frequenting buds of peony and royal lily. *Ent. Mon. Mag.* **92,** 405.

The ant *Lasius niger* is recorded as frequently visiting buds of peonies and royal lilies, while the ant *Lasius flavus*, in the same garden, is not.

Lever, R. A., Armour, C. J. & Thompson, H. V. (1957). Myxomatosis and the fox. *Agriculture*, **64**, 105-111.

The food content of eighty foxes collected from areas to which myxomatosis had spread showed that they were still eating some rabbits, but voles (chiefly *Microtus agrestis*) sheep (some carrion), woodmice, brown rats, poultry, small birds and beetles were all taken fairly frequently.

Lloyd, S. (1957). Enemies of dragonflies. *Trans. Herts. Nat. Hist. Soc.* **24**, 226-229.

A summary of the vertebrate and arthropod predators of the Odonata.

Marshall, S. M. & Orr, A. P. (1956). On the biology of *Calanus finmarchicus*. IX. Feeding and digestion in the young stages. *J. Mar. Biol. Ass. U.K.* **35**, 587-603.

Nauplii and early copepodites of *Calanus* were fed on radioactive cultures of diatoms and phytoflagellates and the food uptake and volumes filtered were measured. The filtering appendages in described Nauplius I and II do not feed. Nauplius III can filter up to a maximum of 1 ml in 24 h, and can eat organisms of up to 20 μ.

Owen, D. F. (1956). Insects taken by herons. *Ent. Mon. Mag.* **92**, 384.

A list of insects taken from the stomachs of nestling herons, *Ardea cinerea cinerea*, is given. Dragon-flies and beetles were prominent in the samples.

Parmenter, L. (1957). Some predators of Aphides with a key to the genera and some species of the family Chamaemyiidae found in Britain. *Ent. Rec.* **69**, 95-96.

Includes keys to the three British genera and to species of *Leucopis* and *Parochthiphila* and lists the prey of five species of *Chamaemyia* and *Leucopis*.

Rao, K. V. N. & Rao, K. P. (1957). Differences in the food of the young and the adult Indian mackerel, *Rastrelliger kanagurta* (Cuv.). *Nature, Lond.* **180**, 711-712.

When longer than 90 mm plankton forms the principal food. Below this size feeding is selective, and fish larvae form staple diet. Growth of gut is allometric, and change in diet coincides with change of relative growth rate of gut.

Richards, O. W. (1957). A solitary wasp which preys on ants. *Ent. Mon. Mag.* **93**, 23.

The sphecid wasp *Tracheliodes 5-notatus* was noted apparently feeding on the ant *Tapinoma erraticum*.

Sankey, J. H. P. (1956). *Empis tessellata* F. (Dipt., Empididae) preying on *Tipula vernalis* Meig. *Ent. Mon. Mag.* **92**, 307.

The fresh dead weight of each insect is recorded.

Scudder, G. G. E. (1957). *Picromerus bidens* (L.) (Hem., Pentatomidae) preying on larvae of *Rhadinoceraea micans* (Klug.) (Hym., Tenthredinidae). *Ent. Mon. Mag.* **93**, 10.

The pentatomid bug *Picromerus bidens* is recorded as feeding on the sawfly larvae of *Rhadinoceraea micans*.

Wayman, C. (1957). Note on the occurrence of *Cryptophagus subfumatus* Kraatz (Col., Cryptophagidae) on Californian seedless raisins. *Ent. Mon. Mag.* **93**, 11-12.

The beetle *Cryptophagus subfumatus* Kraatz is recorded as a breeding infestation of raisins stored in a warehouse. It was considered that the height to which the containers were stacked damaged the containers and allowed entry of the beetles.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Anderson, A. (1957). A census of fulmars on Hirta, St. Kilda, in July 1956. *Scot. Nat.* **69**, 113-116.

An estimate of 19 400 pairs, coinciding closely with the previous estimate in 1949.

Armstrong, E. A. (1957). Birds of the Aran islands. *Irish Nat. J.* **12,** 207-208.
Notes on changes since 1945.

Bagenal, T. B. (1957). The vertical range of some littoral animals on St Kilda. *Scot. Nat.* **69,** 50-51.
Examples of littoral animals being found high up inland.

Baynes, E. S. A. (1957). Report on migrant insects in Ireland for 1956. *Irish Nat. J.* **12,** 145-146.
1956 was a disappointing year, and records were only received for Lepidoptera (11 species).

Beven, G. (1957). The distribution of the grey squirrel in the London area (1953-56). *Lond. Nat.* **36** (1956), 6-11.
Grey squirrels, absent from the central parks, are still common in more rural suburbs and to within 3 miles of St Paul's. 70% habitat records are in woods and parks, 26% in gardens. Some evidence of decrease.

Birkett, N. L. (1956). Some observations on a flight of *Bombus lucorum* L. (Hym., Bombidae). *Ent. Mon. Mag.* **92,** 333.
The bees were observed flying along the coastline in some numbers.

Bishop, M. W. H. & Crisp, D. J. (1957). The australasian barnacle, *Elminius modestus*, in France. *Nature, Lond.* **179,** 482-483.
Recorded from several localities. Map given. Origin discussed.

Bolster, G. C. & Bridger, J. P. (1957). Nature of spawning area in herrings. *Nature, Lond.* **179,** 638.
Spawn found in fish stomachs, and with a grab. It was attached to flints. Maximum concentration found in an area two miles by four hundred yards long. The long axis in line with tidal movement.

Bourne, W. R. P. (1957). The birds of the island of Rhum. *Scot. Nat.* **69,** 21-31.
Systematic list of the birds of a Hebridean island which has just become a National Nature Reserve.

Boyd, J. M. (1956). The Lumbricidae in the Hebrides. II—Geographical distribution. *Scot. Nat.* **68,** 165-172.
Seventeen species are recorded.

Boyd, J. M. (1957). Lumbricidae at Boreray, St Kilda. *Glasgow Nat.* **17,** 280-281.
Two species of earthworms noted.

Boyd, J. M., Tewnion, A. & Wallace, D. I. M. (1957). The birds of St Kilda, midsummer 1956. *Scot. Nat.* **69,** 94-112.
Notes on fifty-five species, with special reference to breeding populations and migration.

Broch, H. (1957). The northern octocoral, *Paragorgia arborea* (L.), in sub-antarctic waters. *Nature, Lond.* **179,** 1356.
Establishes this as a bipolar species at present.

Burns, P. S. (1957). Rook and jackdaw roosts around Bishop's Stortford. *Bird Study,* **4,** 62-71.
Discusses significance of roosts in relation to residents and winter migrants and to the feeding habits of the birds.

Burton, J. F. & Owen, D. F. (1957). The census of heronries 1955-56. *Bird Study,* **4,** 121-124.
Further analysis of census data using new methods, indicating progressive decrease since 1954.

Condry, W. (**1957**). Mammals recorded in an area of West Wales. *Nature in Wales*, **3**, 461-463.
Records thirty-one species from an area around the Dovey Estuary, including the red form of the polecat.

Darlington, A. [**1957**]. The status of the rook as a nesting species in Essex. *Essex Bird Rep.* **1956**, 51-53.
In Essex in 1956 18 252 pairs of nesting rooks were counted in 822 rookeries, a density of 24·26 breeding birds per square mile. Most of the breeding population was concentrated near human habitations in the west and centre of the country, in the upper river valleys at an altitude of 150-200 ft, and avoiding the London suburbs, the chalk escarpment and the coastal strips.

de Worms, C. G. M. (**1957**). The moths of London and its surroundings. *Lond. Nat.* **36** (1956), 59-99.
Notes on localities, abundance, food plants and seasonal occurrence of Geometridae (cf. 1956, *Lond. Nat.* **35**, 33-76, abstr. 1957, *J. Anim. Ecol.* **26**, 232).

Delany, M. J. (**1957**). The small mammals of a Dunbartonshire oakwood. *Glasgow Nat.* **17**, 272-278.
Mainly *Apodemus* and *Clethrionomys*, which shared habitat preferences for different parts of the wood.

Dorward, D. F. (**1957**). The night-heron colony in the Edinburgh Zoo. *Scot. Nat.* **69**, 32-36.
Escapes from a free-living colony at the zoo may be responsible for the striking recent increase in records of this vagrant in the British Isles. Unfortunately the birds have not hitherto been colour-ringed.

Eggeling, W. J. (**1956**). A list of the birds recorded from the Isle of May. *Scot. Nat.* **68**, 127-156.
A complete systematic list of the birds recorded from this well-known migration station in the Firth of Forth.

Eggeling, W. J. (**1957**). Spiders and harvestmen recorded from the Isle of May. *Scot. Nat.* **69**, 51-52.
Twenty-three species of spider, three of harvestmen.

Eggeling, W. J. (**1957**). The mammals of the Isle of May. *Scot. Nat.* **69**, 71-74.
Notes on the mammals of this island in the Firth of Forth, of which the rabbit and the house-mouse are the only two breeding at present.

Eggeling, W. J. (**1957**). A list of the butterflies and moths of the Isle of May. *Scot. Nat.* **69**, 75-83.
Nine butterflies and 110 moths, including Microlepidoptera, recorded from this island in the Firth of Forth.

Fraser, A. C. [**1956**]. Mammals of Middle Thames. *Middle-Thames Nat.* **8** (1955), 7-10.
A list, giving abundance, of some forty mammals recorded from Buckinghamshire south of the northern escarpment of the Chilterns and Berkshire east of the river Loddon.

Friend, G. F. (**1956**). A new sub-species of charr from Lock Eck. *Glasgow Nat.* **17**, 219-20.
Salvelinus alpinus youngeri from a Cowal, Argyllshire, loch.

Frost, W. E. (**1957**). First record of the elver of the African eel *Anguilla nebulosa labiata* (Peters). *Nature, Lond.* **179**, 594.
Two specimens from Tanganyika.

Gibson, J. A. (**1957**). The 1955 census of gannets (*Sula bassana*) on Ailsa Craig. *Glasgow Bird Bull.* **6,** 12-13.
The population was estimated at 10 402 pairs, an increase of nearly 2000 on 1954.

Gibson, J. A. (**1957**). Notes on the birds of the Great Cumbrae. *Glasgow Bird Bull.* **6,** 5-6.
Brief notes on the breeding and other birds of this island in the Firth of Clyde since 1942.

Gordon, I. (**1956**). *Paramola cuvieri* (Risso), a crab new to the Orkneys, Shetlands and Norway. *Nature, Lond.* **178,** 1184-1185.
An account of some recent records.

Goto, H. E. (**1957**). Some further Collembola from Shillay, Outer Hebrides. *Scot. Nat.* **69,** 1-10.
Nineteen species, with a full description and illustration of *Hypogastrura* (*Ceratophysella*) *scotica* which had never been adequately figured or described.

Gotto, R. V. (**1957**). A cyclopoid copepod new to British waters, with a note on its structure. *Irish Nat. J.* **12,** 138.
Lichomolgus marginatus on *Ascidia virginea* in Strangford Lough, Co. Down.

Grainger, J. N. R. (**1957**). Further observations on the planktonic copepods of Irish lakes. *Irish Nat. J.* **12** (5), 129-131.
Species of *Diaptomus* in lakes in Cork and Kerry.

Hager, P. D. (**1957**). Badgers in the N.W. Herts/Bucks area of the Chilterns. (*Meles meles meles* (L.)). *Trans. Herts. Nat. Hist. Soc.* **24,** 201-208.
Field notes on the distribution and sites of sets, signs of badgers and their relationship with foxes.

Hunter, W. R. & Hunter, M. R. (**1956**). A note on *Plumatella* and *Ancylus* in a mountain lochan. *Glasgow Nat.* **17,** 241-242.
Notes on habitat and breeding of a bryozoan and a freshwater limpet in a lochan 1450 ft up in Skye.

Hunter, W. R. & Warwick, T. (**1957**). Records of '*Potamopyrgus jenkinsi*' (Smith) in Scottish fresh waters over fifty years (1906-56). *Proc. Roy. Soc. Edinb.* B **66,** 360-373.
Traces dispersal of this snail across Scotland largely from the Tay.

Kent, A. K. (**1957**). The breeding birds of a North Pembrokeshire Farm. *Nature in Wales,* **3,** 421-425.
Of 81 species recorded on the farm, 35 breed. The dominant species is the Chaffinch. The larger members of the thrush family are almost absent. Other species discussed are yellow bunting, long-tailed tit, woodlark, spotted flycatcher, lapwing, owls and buzzard.

Kettlewell, H. B. D. (**1957**). *Lithophane lapidea* Hübner (Lep., Noctuidae) breeding in Britain. *Entomologist,* **90,** 1-8.
Evidence of breeding by this Mediterranean species in Britain was obtained for the first time in October 1956, when large numbers of females were trapped among *Cupressus* in the Isle of Wight and eggs were laid on the foliage.

Kevan, D. K. McE. (**1957**). Wiltshire Orthopteroids. *Entomologist,* **90,** 12-16.
Lists, with localities, habitats and dates, for Dictyoptera, Orthoptera and Dermaptera, mostly based on collections in 1956. Several new county records and confirmations of previously doubtful records.

Leatherdale, D. (1957). The incidence of some gall-causing insects and mites in south Oxfordshire and central Berkshire in 1956. *Ent. Mon. Mag.* **93,** 26-29.
Altogether forty-eight species of gall-formers belonging to Hemiptera-Homoptera, Lepidoptera, Coleoptera, Hymenoptera (Tenthredinidae, Cynipidae), Diptera and Acarina are recorded from this area.

Mackenzie, J. M. D. (1957). Pied flycatchers in Perthshire. *Scot. Nat.* **69,** 45-49.
A review of the colonization of Perthshire by *Muscicapa hypoleuca* since 1950.

Massee, A. M. (1956). Notes on some interesting insects observed in 1955. *Rep. E. Malling Res. Sta.* A **39** (1955), 131-134.
Comments on some of the insects collected from fruit trees in south-east England in 1955.

Massee, A. M. (1957). Notes on some interesting insects observed in 1956. *Rep. E. Malling Res. Sta.* A **40** (1956), 131-134.
Comments on some of the insects collected from fruit trees in south-east England in 1956.

Menzies, W. J. M. & Shearer, W. M. (1957). Long-distance migration of salmon. *Nature, Lond.* **179,** 790.
Salmon marked in Scotland recovered in Greenland.

Miles, P. M. (1957). Indigestibility of the eggs of the common frog (*Rana temporaria*) to the common heron (*Ardea c. cinerea*). *Nature in Wales,* **3,** 426-428.
Observations on frogs and herons at Trawscoed Lake in Cardiganshire.

Nesbitt, L. (1957). Heronry census in Armagh district. *Irish Nat. J.* **12,** 215-216.
Figures for eight heronries for each year, 1953-1957.

Niblett, M. (1957). The gall midges (Cecidomyiidae) of Bookham Common. *Lond. Nat.* **36** (1956), 51-54.
Lists some seventy species since 1929 with food plants, situations of galls and pupae and dates for larvae and adults.

Nisbet, I. C. T. (1957). Wader migration at Cambridge sewage farm. *Bird Study,* **4,** 131-148.
Analyses passage of twenty-four species of waders on the basis of 4-5 day periods, correlating migration times with extents of breeding range, wing size and timing of the breeding cycle. Discusses origin of waders passing Cambridge.

O'Rourke, F. J. (1957). *Bombus distinguendus* Mor., one of the rarer Irish bumble bees. *Irish Nat. J.* **12,** 187-189.
A bee which may be at the limit of its climatic tolerance in Ireland.

Parmenter, L. (1957). Diptera of the chalk downs in May, about Old Coulsdon, Surrey. *Ent. Rec.* **69,** 126-130.
A list of some 170 species found on downland and hedgerows and in woodland, with others of species found at the flowers of several herbs and shrubs and of the prey taken by *Empis femorata* and *Rhamphomyia sulcata.*

Pate, J. S. (1957). The breeding and non-breeding bird population of Netherleigh grounds, Belmont, Belfast. *Irish Nat. J.* **12,** 153-162.
Detailed surveys of the nesting population, with maps of nest sites, and of the non-breeding resident bird population of 20 acres of parkland, for 1955-56.

Peters, J. V. (1957). Birds observed at Annagh and Brackagh mosses, Co. Armagh. *Irish Nat. J.* **12,** 168-71.
Systematic list of the birds of a fen swamp and a raised bog remnant on the edge of Lough Neagh.

Ranade, M. R. (1956). Occurrence of *Polydora pulchra* Carrazi in British waters. *Nature, Lond.* **178,** 929.
First record of this polychaete in Irish Sea. *Nature, Lond.* **178,** 929.

Rice, C. (1956). The corn bunting in Wiltshire: report of an inquiry, conducted during 1951-52-53-54. *Wiltsh. Archaeol. Nat. Hist. Mag.* **56,** 430-36.
A survey of the local distribution of the corn bunting throughout the county.

Richardson, A. (1957). *Pontia daplidice* L. in Gloucestershire. *Entomologist,* **90,** 51.
Two specimens were active on 4 August 1956 in a locality where *Reseda alba* grows plentifully.

Richardson, R. A., Seago, M. J. & Church, A. C. (1957). Collared doves in Norfolk. *Norfolk Bird Rep.* **1956,** 21-23.
An account of this new British breeding species (*Streptopelia decaocto*) at its first breeding site in the British Isles in 1955 and 1956, in north Norfolk.

Richardson, R. A., Seago, M. J. & Church, A. C. (1957). Collared doves in Norfolk: a bird new to the British list. *Brit. Birds,* **50,** 239-246.
Two or three pairs nested successfully, and one reared three broods. Field notes on the habitat and habits of the Norfolk birds are given.

Robertson, T. (1956). Records of the arrival of summer birds—summary of results. *Glasgow Nat.* **17,** 236-240.
A summary of records of twenty-five species in the Clyde area from 1893 to 1956.

Ruttledge, R. F. (1957). The birds of Inishbofin, Co. Galway with some notes on those of Inishshark. *Bird Study,* **4,** 71-80.
Classified lists with some notes on changes of status.

Ruttledge, R. F. (1957). The occurrences by months and counties of the smew and spotted redshank in Ireland. *Irish Nat. J.* **12,** 131-133.
Mergus albellus has occurred mainly in Ulster and Leinster from December to February, *Tringa erythropus* mainly in Leinster and Connaught from August to February. The latter has occurred in every month except June.

Ruttledge, R. F. (1957). The wader migration in Ireland in autumn, 1956. *Irish Nat. J.* **12,** 208-213.
Detailed notes on a dozen species.

Sage, B. L. (1957). The history and distribution of the great crested grebe in Hertfordshire. *Trans. Herts. Nat. Hist. Soc.* **24,** 218-223.
Summarizes the population changes since 1867, when three pairs probably bred, with notes on migration, wintering and flocking.

Sage, B. L. (1957). Notes on dragonflies in Wales in 1956. *Nature in Wales,* **3,** 434-435.
Records from Breconshire, Merionethshire, Pembrokeshire, Carmarthenshire and Cardiganshire.

Sage, B. L. (1957). A contribution to the entomology of Scolt Head Island, Norfolk. *Entomologist,* **90,** 123-124.
Lists of eleven beetles and five spiders collected in May 1956, with habitats.

Salmon, H. M. (1957). Ornithological notes. *Trans. Cardiff Nat. Soc.* **84,** 15-17.
Notes on forty-nine of the more interesting species observed in Glamorgan and eight in Monmouthshire.

Savory, T. H. & Le Gros, A. E. (1957). The Arachnida of London. *Lond. Nat.* **36** (1956), 41-50.

Lists, with localities, 130 Araneae, nine Opiliones, six Pseudoscorpiones from London postal area. Discusses with reference to wider distribution, to smoke pollution and urbanization. Little parasitism but predation by the wasp, *Trypoxylon figulus*, is important.

Scudder, G. G. E. (1957). The subspecies of *Ischnodemus sabuleti* (Fallén) (Hem., Lygaeidae). *Ent. Mon. Mag.* **93,** 14-18.

The two subspecies *Ischnodemus sabuleti quadratus* and *I. sabuleti sabuleti* are analysed with respect to their European distribution, and it is concluded that the former subspecies is a northern form while the latter has a north Mediterranean distribution.

Smith, R. W. J. (1957). 'Northern' golden plovers in Midlothian during spring. *Scot. Nat.* **69,** 84-88.

Field notes on birds approximating to the form *Charadrius apricarius altifrons*.

Southwood, T. R. E. & Johnson, C. G. (1957). Some records of insect flight activity in May 1954 with particular reference to the massed flights of Coleoptera and Heteroptera from concealing habitats. *Ent. Mon. Mag.* **93,** 121-126.

A propeller type suction trap was operated in a wheat field for a period during May and records are given for Coleoptera, Hemiptera, Hymenoptera and Diptera.

Swan, M. A. (1957). Specimens of char from Shetland and the Faroes. *Scot. Nat.* **69,** 67-70.

The Shetland char (*Salvelinus gracillimus*), in the Loch of Girlsta was believed extinct, but is thriving. Its title to specific rank is questionable.

Thompson, D. Nethersole- (1957). Ecological notes on golden plovers in the Cairngorms. *Scot. Nat.* **69,** 119-120.

Notes on nesting habitat.

Unsworth, C. F. [1957]. Fauna of Leasowe Common (1953-56). *Proc. Liverpool Nat. Fld. Cl.* **1956,** 24-25.

Notes, mainly on birds, on a grassy common on the coast of the Wirral, Cheshire.

Vanucci, M. (1956). Notes on the hydromedusae of the Clyde sea area with new distribution records. *Glasgow Nat.* **17,** 243-49, 281.

The relative abundance of species collected in April-May 1956 compared with previous periods suggests a growing influx of Atlantic water in the Clyde area.

Walls F. D. E. & Thomas H. T. (1957). Notes on the birds of the Ardlamont peninsula, south Argyll. *Glasgow Bird Bull.* **6,** 6-12.

A survey of a tract of country whose bird life has been considerably disturbed by its use as a battle training ground and subsequent re-afforestation.

Watson A. (1956). The Hatton Castle rookery. *Scot. Nat.* **68,** 162-164.

The number of nests in the largest rookery in the British Isles was about 5800 in 1956. About 10 000 young rooks were shot but at least 1500 survived.

Went, A. E. J. (1957). The pike in Ireland. *Irish Nat. J.* **12,** 177-182.

Summarizes the evidence for the pike having been introduced in Ireland during the Middle Ages and spread over the country especially during the past two hundred years.

Went, A. E. J. & Twomey, E. (1957). Notes on Irish char, *Salvelinus colii* Gunther: VI. *Irish Nat. J.* **12,** 205-206.

Notes on char from Loughs Corrib and Fad, with descriptions and measurements.

Willgohs, J. F. (1957). Occurrence of the leathery turtle in the northern North Sea, and off western Norway. *Nature, Lond.* **179,** 163-164.
Records of specimens of *Dermochelys coriacea.*

Williams, T. S. (1956). Notes on the bird life of the City of Chester. *Proc. Liverpool Nat. Fld. Cl.* **1955,** 21-32.
Continuing the systematic list of birds found in the city, with a summary of increases and decreases.

Yeo, P. F. (1957). Bees and wasps in Bushey Park and at Hampton Hill, Middlesex. *Lond. Nat.* **36** (1956), 16-24.
Lists 102 species mostly in Bushey Park and a private garden near by, 1948 to 1953, and compares with an earlier survey of Hampstead Heath. Habitat notes.

6. STUDIES ON BEHAVIOUR

Armstrong, E. A. (1956). Distraction display and the human predator. *Ibis,* **98,** 641-654.
Concludes that the size of human populations and man's mentality in the past rule out human interference as an appreciable factor in the evolution of distraction displays. The more specialized displays of birds breeding in the Arctic is attributed to the limited number of predators in high latitudes compared with tropical forest.

Blackith, R. E. (1957). Social facilitation at the nest entrance of some Hymenoptera. *Physiol. Comp. Oecol.* **4,** 388-402.
Demonstrates non-random passage in and out of the nests of wasps and humble bees and suggests that passage is inhibited until sufficient individuals have accumulated to act as a releaser. Discusses observations primarily in relation to behaviour mechanisms.

Driver, R. (1957). Linnets nesting socially in tufts of the common rush. *Brit. Birds,* **50,** 397-398.
Five pairs nested in a disused gravel pit. Many hedgerows and bushes in the vicinity had been uprooted during the previous year.

Hewson, R. (1957). Social flying of ravens. *Brit. Birds,* **50,** 432-434.
Draws attention to gatherings unconnected with feeding or roosting, and suggests they may influence pair formation.

King, J. M. B. (1957). Unusual call-note of green sandpiper. *Brit. Birds,* **50,** 168.
A green sandpiper *Tringa ochropus* which uttered a note like the normal call of a wood sandpiper *T. glareola,* trapped and identified by its measurements, repeated the call on release, and used no other note.

Kramer, G. (1957). Experiments on bird orientation and their interpretation. *Ibis,* **99,** 196-227.
The ability of sun-azimuth orientation has been demonstrated experimentally in four species of wild birds and in homing pigeons. There is strong evidence of night orientation by stars. Experiments supporting the hypothesis of sun-arc navigation are re-analysed, and it is concluded that evidence in its favour is insufficient; an explanation of homing orientation is still lacking. (See also Kramer, G., 1952, *Ibis,* **94,** 265-285. Abstract in 1955, *J. Anim. Ecol.* **24,** 496.)

Lindahl, K. Curry (1956-57). Behaviour of the tropical rock lizard *Agama cyanogaster* (Ruppel) in hot environments. *Ann. Soc. Roy. Belg.* **87,** 45-74.
Discusses behaviour of this lizard basking on rocks in relation to air and substrate temperatures and surveys general problems of the ecology of reptiles in deserts.

Mackenzie, J. M. D. (1957). Treecreepers roosting in Wellingtonias. *Bird Study*, **4,** 94-97.

The habit, now apparently universal, must be of recent acquisition, since no Wellingtonias large enough to provide roosting niches can have existed in Britain earlier than 1890-1900.

Mylne, C. K. (1957). Bond between a captive twite and a free one. *Brit. Birds*, **50,** 171-172.

A juvenile twite was kept in a box near a window indoors overnight, and in the morning another was sitting on the sill outside the closed window in spite of exposure to rain. When the captive was released, their subsequent behaviour suggested they were of the same brood.

Seabrook, T. (1957). The behaviour of house sparrows in the presence of ants. *Brit. Birds*, **50,** 442-443.

On several occasions house sparrows were seen to go to a swarm of ants, stand among them, and then apparently pick something off the lower breast. On one occasion three placed ants on their breasts without rubbing movements.

Simmons, K. E. L. (1957). A review of the anting-behaviour of passerine birds. *Brit. Birds*, **50,** 401-424.

Forms of anting-behaviour, with bibliography, are described. Over 100 species have been recorded as anting, probably true instinctive behaviour which may effect more efficient preening. It is apparently confined to passerine birds.

7. REPORTS OF ORGANIZATIONS

Bardsey Bird and Field Observatory [1957]. 1956 Report. 47 pp.

Besides the usual systematic list of birds and report on birds ringed contains notes on the birds killed at the lighthouse, ectoparasites from birds and mammals and a visit to the small island of Ynys Gwylan Fawr.

Cornwall Bird-watching and Preservation Society (1957). 26th Annual Report, **1956.** 64 pp.

Consists mainly of faunistic and migration notes for Cornwall and the Scilly Isles.

Derbyshire Ornithological Society, The. Report for **1955.** 1956. 23 pp.

Contains a systematic list of birds seen in the county during the year, with supplementary lists of the arrival and departure of migrants.

Essex Bird Watching and Preservation Society [1957]. Essex Bird Report. 68 pp.

In addition to the usual systematic list there are short reports on the arrival and departure of migrants, the Abberton and Romford Ringing Stations, the Bradwell and St Osyth Observatories, the Great Wood Nature Reserve at Hadleigh, and the wildfowl counts, as well as a paper on the breeding status of the rook.

Fair Isle Bird Observatory [1957]. Annual Reports for **1955** and **1956.** 39 pp.

The work done at the observatory continued to consist largely of the study of bird migration, also of the skuas breeding on the island and of bird ectoparasites. In 1955 a mercury vapour moth trap was used in an attempt to correlate bird and moth movements.

Fair Isle Bird Observatory Bulletin, 3 (3), 109-160. 1957.

Includes short papers on migration at Great Saltee (Co. Wexford), Portland Bill (Dorset) and Unst (Shetland), summer bird notes from Foula (Shetland), movements of redwings in autumn 1956, and breeding season studies of great and arctic skuas on Fair Isle.

Glasgow Bird Bulletin. Vol. **5,** 44 pp. 1956.

Includes papers or notes on the birds of East Kilbride (Lanarkshire), Sanda, Sheep Island and Glunimore (Kintyre peninsula, Argyll), Rosneath (Dunbartonshire) and Pabbay (Skye).

Lundy Field Society (1957). Tenth Annual Report (1956). 77 pp. Price 5s.

In addition to the usual systematic notes on birds and mammals, recoveries of ringed birds, work on nesting sea birds and ectoparasites, contains a number of special papers surveying work over the past ten years, viz. the results of ringing guillemots, razorbills and shags; gull populations; results of measuring and weighing blackbirds and some migrant species; and a summary of work on some breeding birds.

Mid-Somerset Naturalist Society (1955). Fourth Report and Reference Book, **1954.** 77 pp.

Faunistic notes on birds, mammals and insects, mainly Lepidoptera.

Sussex Bird Report, 1955. 20 pp. 5s.

Consists almost entirely of a systematic list.

BRITISH ECOLOGICAL SOCIETY

SPRING MEETING IN CAMBRIDGE
27-29 March 1957

The meeting opened on the evening of 27 March with an informal soirée in King's College. About fifty members and guests enjoyed an agreeable social evening.

The next morning about forty members and guests assembled in the Department of Zoology where they were welcomed by Dr George Salt before listening to four papers on ecology outside the British Isles. Dr Salt began with an account of his investigations into the relationships between *Acacia drepanolobium* and ants of the genus *Crematogaster* in the Athi Plains, East Africa. The acacias produce thorns whose bases swell to about walnut size. The ants gnaw out the centres of these swellings leaving a hard hollow shell in which they live. The ants feed on the folia nectaries of the acacia, and form polycalic colonies, each colony inhabiting one tree or a group of adjacent trees. Dr Salt presented the results of censuses on the populations of ants and their different castes and stages. He concluded that the ants and acacias lived in symbiosis as the ants gave the trees some protection against defoliating caterpillars and other insects. This question of the symbiotic nature of the relationship gave rise to a short discussion in which Dr Potts and Mr Gilson took part. Dr R. W. J. Keay then presented his paper on ecological change in African Savanna vegetation. Savanna is a characteristic vegetation with a distinct flora covering large areas of Africa under a wide range of rainfalls. It varies from nearly treeless grassland to open woodland and is dominated by large tussocky grasses. Fire appears to be one of the most important ecological factors and is nowadays nearly always caused by man. Dr Keay then went on to describe a number of examples from Nigeria, paying particular attention to the distinct boundaries between rain forest and savanna, and also giving an account of experiments with different burning treatments. Late burning tends to destroy the tree layer but early burning is more destructive to the grasses. Drs Watt, Richards, Hope-Simpson and Potts took part in the discussion and raised, among other topics, the problem of the seed source for regenerating trees and possible causes of fires.

After a mid-morning break for coffee Dr E. J. Moynahan read his paper on ecological aspects of the pigmentation of the human skin. He first described the formation of melanin by the melanocytes in the basal layer of the skin, and the variations in amount of melanin in different parts of the skin, in different races and in different individuals. The enzyme tyrosinase, which is absent in albinos, is necessary for the synthesis of melanin from tyrosine. Hormones from the pituitary and adrenals influence the formation of melanin. Dr Moynahan then ended his paper with a brief discussion of the ecological significance of melanin. Ultra-violet light causes sunburn and skin cancer but also is necessary for vitamin D synthesis. Sunburn from exposure to U.V. light can be detrimental to sweat production which is important in protecting the body from heat stroke. In cloudy regions vitamin D synthesis may be more important than the risk of heat stroke.

In the last paper of the morning Dr R. Bainbridge described his observations and experiments on plankton movements in relation to polarized light in Bermuda. Dr Bainbridge first described laboratory experiments with plankton crustacea which showed that some species tended to swim at right-angles to the plane of polarization. He then described some observations on the direction taken by individual animals released in the sea and followed by an observer with skin diving equipment. These animals tended to swim in the plane of the polarized light from the sky. In the discussion following the paper Mr Gilson mentioned the fact that shoals of Mysids do swim to and fro.

The meeting was resumed after lunch with a paper by Mr R. C. Fisher entitled 'Darwin and the flightless beetles of Madeira'. Wollaston was the first to observe that a high proportion of the beetles in Madeira were flightless and later Darwin used this as an

example of adaptation to island life. Mr Fisher described some results obtained by him on an expedition to the Madeira islands. An analysis of samples from several habitats over an altitude range on Madeira and from two small neighbouring desert islands showed that a large proportion of the individual beetles were apterous but many species were not. It appeared that wings had been lost or retained as an adaption to a specific microhabitat or ecological niche and not, as Darwin thought, to the dangers of being blown away from an island or mountainous environment. In the discussion Dr Holdgate presented some observations on endemic species on Tristan da Cunha and Dr Williams wondered how much flying many species of beetles in fact did.

The afternoon session ended with an account by Dr H. B. Cott of the ecology of the Nile crocodile. The paper included a considerable amount of factual observation on the natural history of the crocodile that were illustrated by a magnificent series of photographs, mostly obtained at close quarters from a hide. The crocodiles feed in the water at night and sunbathe during the day, often half in the water during the hottest period when the mouth may be gaped also as a cooling mechanism. Dr Cott described and illustrated the three methods of locomotion on land, and the average rates of growth. Breeding is correlated with low water levels and from forty to ninety eggs are laid, buried not far from water. The young crocodiles feed on invertebrates but then change to fish, but the largest individuals also eat vertebrates other than fish.

Members then took an informal tea in the adjoining laboratory and at the same time examined a number of exhibits provided by the Zoology and Botany Departments, many of which illustrated papers that were being read at the meeting.

On the morning of 29 March about forty members assembled and began the day's agenda by hearing a report from Mr Summerhayes on the Society's financial situation and the accounts for 1956. There was a deficit in the Revenue Account for the year of about £800 due largely to increases in the costs of the Journals. Dr Mellanby, Dr Goodhart and Mr Gilson initiated some discussion on ways of reducing the costs of the Journals such as shortening the length of the Reports of Meetings of the Society. On the proposal of Mr Gilson, seconded by Dr Evans, the accounts were adopted and the Honorary Treasurers thanked for their Report.

The proceedings then continued with two papers on the ecological significance of diurnal rhythms. Dr J. L. Cloudsley-Thompson gave the first paper, entitled 'Diurnal rhythms and water relations in terrestrial Arthropoda'. Terrestrial arthropods can be divided into two groups, firstly those animals such as wood-lice that lose water rapidly in dry air and are therefore restricted to damp and dark habitats, at least during the day, and secondly those that are covered by a waxy layer that protects them against desiccation. The intensity of the responses of various species of wood-lice to humidity, and the intensity of their nocturnalism, are correlated with their ability to withstand water loss by transpiration. Dr Cloudesley-Thompson illustrated the conflict between the incompatible requirements of respiration and the prevention of water loss by a comparison between two spiders of the genus *Amaurobius* (= *Ciniflo*). Observations in Tunisia showed that there is no fundamental difference as regards water relations and diurnal activity rhythms between the fauna of deserts and temperate regions.

Dr Janet Harker followed with a general account of the problems of diurnal rhythms entitled 'The adaptability of diurnal rhythms'. A 24-hour rhythm has shown to occur in a wide range of physiological activities. Many of these, such as bird song, appear to be controlled or influenced by light periodicity, and temperature changes have little effect, but there often appears to be a hierarchy of controlling factors. Dr Harker described some laboratory experiments under carefully controlled conditions where the normal rhythm had been changed, and others where it was maintained under apparently constant environmental conditions for long periods. A lively discussion followed the paper, in which Mr Gilson, Dr Waloff, Dr Haskell and Dr Moynahan took part. The difficulty of eliminating all diurnally varying factors in the controlled experiments was emphasized.

The second half of the morning was devoted to two papers on analogous botanical problems. Dr A. J. Rutter and Mrs K. Sands discussed leaf-water deficit and its significance in *Pinus sylvestris*. The measurement of stomatal opening, transpiration rate and leaf-water deficit through 24-hour periods in 2-3 year old pines at four levels of soil

moisture content were described. It was found difficult to relate leaf-water deficit closely to soil moisture content but certain conclusions were drawn. The leaf-water deficit might frequently restrict the net assimilation rate in dry soils, and it was shown that *Calluna* and *Molinia* might well influence young pine trees in a dry summer through competition for water. Professor Varley commented that the effects of insect attack might be correlated with humidity and Dr Whitehead discussed the root-shoot ratio aspect of the problem.

Dr G. C. Evans presented a paper entitled 'Autecological problems and the production of controlled environments in the laboratory'. Professor Clapham's Presidential Address was recalled, which had made a plea for observations and experiments with plants under controlled or partly controlled conditions. The range of completely artificial environments available is usually limited by the difficulty of generating illumination equivalent to full sunlight. Woodland plants are therefore particular suitable subjects for investigation. Dr Evans described a relatively inexpensive controlled environment cabinet (which he had also demonstrated to some members the previous afternoon). *Impatiens parviflora* had been successfully grown to maturity in a state similar to that found in woodland shade and subject to variations in individual environmental factors. Dr Evans also discussed the problem of the measurement of factors such as light and their integration over a long period. In the discussion in which Professor Varley and Dr Hughes took part, the importance of artificially varying environmental factors in field experiments was stressed.

On the afternoon of the 29th about sixteen members went by bus to the Entomological Field Station in Storey's Way and the Ornithological Field Station at Madingley. Dr Kennedy showed us the rearing experiments with cabbage-white butterflies, investigations into the flying behaviour of aphids in relation to environmental factors and some of the ingenious apparatus used in these and other investigations and also provided a welcome cup of tea. At Madingley, under the guidance of Dr Hynde and his colleagues, we were shown aviaries where hybrid finches were being bred, the recording and analysis of bird song and the teaching of songs to young birds, observations of the feeding behaviour of birds and breeding behaviour of hamsters.

The Society is very grateful to all our hosts at Cambridge, to the Provost and Fellows of King's College for providing accommodation for members and for the soirée, to Professor Sir James Gray for the hospitality of his Department and to Dr Salt who made most of the local arrangements. These people and the others from Cambridge who read papers or demonstrated their work provided a very enjoyable and stimulating meeting and ample evidence of vigorous investigations especially in the experimental approach to ecology.

SUMMER MEETING AT EXETER

10-15 July 1957

Members assembling at Mardon Hall, University of Exeter, for the Summer Meeting were immediately impressed by the attractive setting of the University buildings and the dignified trees of the arboretum near by. The meeting proved a delightful one from the moment of arrival onwards—full of variety, interest and enjoyment. Comfortable accommodation, excellent organization and kind hospitality combined to achieve this successful result. Over sixty members and guests attended.

A small party of members who had arrived by lunch-time on Wednesday, 10 July, was taken in the afternoon to inspect Dawlish Warren, a double sand spit extending across the mouth of the River Exe. From the car park (where, thanks to the shade cast by parked cars, *Trigonella ornithopodioides* was seen flowering, and still freshly green after prolonged drought) a short walk took the party on to the Outer Warren beyond the region most densely colonized by holiday-makers. Here Mr T. J. Wallace pointed out the extent of marine erosion of the foredunes, and the results of action taken by the railway

authorities to halt this by the erection of brushwood fences. The fame of the Warren as a locality in which a remarkable variety of unusual species is concentrated in a small area was readily appreciated, and of the many interesting plants seen mention may be made of *Romulea columnae*, the Warren Crocus (of which, however, only remains of the early flowers were visible), *Briza maxima* and the tall bushes of *Lupinus arboreus* forming dense scrub on the fixed dunes. The presence on the Inner Warren of *Callunetum* and damp hollows occupied by *Salix atrocinerea*, and the occurrence of two species of *Sphagnum* amongst *Calluna* and *Erica tetralix*, aroused interest as indications of the potential development of an area now largely given over to a golf course. Among insects taken were *Notonecta viridis* and *Saldula palustris*, the latter hitherto unrecorded for the Vice-County of S. Devon. The saltings yielded *Zostera hornemanniana*, numerous species of *Salicornia*, and *Spartina maritima* as well as *S. townsendii*.

By invitation of Professor J. Caldwell and Professor L. A. Harvey a soirée was held during the evening, in the Hatherly Biological Laboratories, at which members had the pleasure of meeting the Vice-Chancellor of the University of Exeter, Dr J. W. Cook.

Maps, specimens, books and papers relating to the places to be visited during the meeting were on view, and an exhibit of the Ecology of Braunton Burrows was contributed by Dr A. J. Willis, Professor E. W. Yemm, Dr B. F. Folkes and Dr J. F. Hope-Simpson. Mr T. J. Wallace's exhibit of the Larger Fungi of Sand Dunes was illustrated by very pleasing paintings and colour photographs, and many fine photographs of plants by Dr M. C. F. Proctor were on view. The subjects of other exhibits were Viruses of Tomatoes (Professor J. Caldwell, Dr J. Wilkinson and Miss S. Robb), Mycoses of Animals (Dr G. C. Ainsworth), the Ecology of a Dartmoor Upland Stream (Mrs P. A. Horton), a method for Rapid Estimation of Vegetation for Correlation with Faunistic Studies (Mrs C. Harvey), the Diet of the Buzzard (Mr P. Dare), and *Corrigia vitta* a peculiar parasite of small mammals (Miss N. Taggart).

The expedition to Yarner Wood Nature Reserve on Thursday, 11 July, unfortunately coincided with the end of the drought, but in spite of this and under the umbrella provided by the dense tree canopy, members were given a fascinating tour of the reserve by Dr N. W. Moore and other members of the Nature Conservancy. Much of the wood now consists of *Quercus petraea*, but there is at present little natural regeneration except of *Fagus sylvatica* and *Sorbus aucuparia*. Acting on the assumption that the great dominance of oak is an artefact, experimental plantings are being commenced of several other species, including *Ulmus glabra*, *Alnus glutinosa*, *Corylus avellana* and *Fagus sylvatica*, in an attempt to determine which of these will eventually become incorporated into a mixed wood more nearly resembling the original. Experiments designed to discover the factors preventing regeneration of oak were demonstrated, and accounts given of work in progress on the estimation of populations of small mammals, and on the habits of the various birds which nest in holes in tree trunks. One result of the provision of nesting-boxes at various heights on trees had been the attraction to the area of the pied flycatcher as a breeding species. Among species noted by entomologists were *Gerris gibbifer* on a pool, heavily infected with the mite *Limnochares aquatica* and *Piezodorus lituratus* (Pentatomidae). It was a pleasure to have the Rev. K. Martin in the party on this excursion, and some members had the satisfaction of accompanying him to the place in the wood at which he recorded *Acaena anserinifolia*, where it still flourishes.

A short stop was made at Knighton Heath, where clay pits containing *Utricularia major* and *Hypericum elodes* were examined, around the margin of one of which is a turf composed of *Eleogiton fluitans* and *Galium debile*. A specimen of the dragonfly *Ceriagrion tenellum* was seen, and in a near-by grassy area nests of the ant *Formica exsecta* were shown by Dr G. M. Spooner. The excursion ended with tea at Chudleigh Rocks, where a limestone exposure in the grounds provided bryologists with entertainment until the departure time of the coach.

The excursion to Braunton Burrows on Friday, 12 July, took place in fine weather, the vegetation already showing the benefit of the moisture supplied on the previous day. A short stop at Saunton Cliffs enabled members to see the north end of the dune system, where post-war clearance of mines has disrupted the foredunes. Behind these, slacks containing a clearly defined community of *Leontodon lysseri*, *Plantago coronopus*, *Juncus*

acutus, *Anagallis tenella*, *Gentiana amarella*, *Centaurea pulchellum*, *Carex arenaria*, *Potentilla anserina*, *Hydrocotyle vulgaris*, etc., were examined. Specimens of *Matthiola sinuata* were also seen in this area.

After lunch near the southern end of the dunes, a brief description of the ecology of the Burrows was given by Dr A. D. Willis and relays of transport ferried members to interesting sites. Most members saw the area over which U-shaped dunes move inland at a rate of about 50 ft in 12 years. Behind the U, erosion down to a water table takes place, with subsequent colonization by species typical of damp dune slacks, such as *Juncus acutus*, *Salix repens*, *Epipactis palustris*, *Orchis praetermissa*, *O. strictifolia*, with *Holoschoenus vulgaris* a striking member of the community. *Salix atrocinerea* and *Ligustrum vulgare* form a rather conspicuous semi-circle of scrub behind the crescent of the U-dune. Beyond the landward spill-out of the dunes is an extensive area of dune pasture with an underlying dome-shaped water table where, besides *Thymus drucei*, *Festuca rubra* and *Carex arenaria*, rare species such as *Teucrium scordium* and *Equisetum variegatum* are to be found. The following list of noteworthy insects observed on the Burrows includes two new vice-county records:

Ceartoscirta cincta (Saldidae)	*Notiophilus aquaticus* (Carabidae)
Hydrometra stagnorum	*Panageus crux-major* ,,
Chrysomela populi (Chrysomelidae)	*Poecilus coerulescens* ,,
Myrmeleetettix maculatus (Acrididae)	*Saldula saltatoria*

A comment that the last of these occurred in an unusually dry habitat was echoed by botanists with regard to the presence at the same place of *Anagallis tenella*.

On the way to Dartmoor, on Saturday, 13 July, a halt was made at Steps Bridge to visit the sun-baked rocks where *Hypericum linarifolium* grows in some abundance, as well as several interesting mosses. Before members re-embarked in the coach a local resident, having correctly divined their interests, produced a live Death's-Head Hawk-Moth for their admiration. The main objective of the excursion was Wistman's Wood, which was reached shortly before lunch-time after a walk across the moor. Ample time allowed members to explore this unusual example of *Quercus robur* wood situated on granite 'clitter' at about 1300 ft, in which the trees although often of considerable girth and with numerous twisted branches are restricted to about 15 ft in height. Striking features are the abundance of species growing epiphytically on the trunks and branches, including *Vaccinium myrtillus*, *Polypodium vulgare*, *Dryopteris spinulosa*, and several mosses, including *Antitrichia curtipendula*. Two species of Tipulids were taken in the wood: *Tipula scripta* and *T. hortulana*, the latter emerging from a pupa in lichen on the oak trunk. On the boulders the following cycle of colonization could be observed:

Stage 1. Scattered bryophyte patches. *Dicranum scoparium* predominant; also *Rhacomitrium heterostichum*, *R. lanuginosum*, *Frullania tamarisci*, *Hypnum cupressiforme*, *Plagiothecium undulatum*.
Stage 2. Closed mat of *Eurhynchium myosuroides* and/or *Rhytidiadelphus loreus*.
Stage 3. Entry, amongst the species of stage 2, of *Polytrichum* spp., *Pleurozium schreberi*, *Pseudoscleropodium purum*, *Hylocomium splendens* and *Sedum anglicum*.

At this stage it appears that the arching growth of *Rhytidiadelphus loreus* loosens the attachment of the mat which frequently then strips clean away from the rock.

Examination of bogs on the opposite side of the valley yielded *Pinguicula lusitanica* in flower.

It was a great pleasure to the Society to have the company on this excursion of four of the members of the Botanical Society of the British Isles, meeting concurrently at Launceston. The credit of discovering the only clump of *Hymenophyllum* to be seen during the afternoon goes to them.

During the evening two striking colour films were shown by Mr Hurrell, in the Hatherly Laboratories. One traced the life of the Dipper through a complete year's cycle, and the other—surely a remarkable achievement in photography—showed the history of a hornet's nest from its very foundation by the queen to its final desertion.

The excursion on Sunday, 14 July, again took us to a Nature Reserve; this time to the

'out-of-door museum' of the Dowlands Landslip near Lyme Regis. After an introductory account by Dr N. W. Moore and instructions on path finding, the Society was swallowed up without trace for the remainder of the day by the dense thicket, to emerge miraculously in twos and threes in the neighbourhood of the coach about the time for departure. Credit and thanks should be accorded to some senior boys of Allhallows School who acted as guides to several of the parties. To explore the reserve, members traversed what must be the thickest jungle in the British Isles, where tall *Fraxinus excelsior* trees are festooned with rope-like lianas of *Clematis vitalba*, worthy of any rain forest. The broken terrain is densely covered with calcicolous shrubs colonizing the exposed chalk, and many of these are thickly overgrown with *Rubia peregrina*. Numerous landslips have occurred in the past along this stretch of coast, the last extensive fall taking place in 1839. The exact age of the re-established vegetation is thus known, and it provides an example of something now extremely hard to find in Britain—a plant community which has throughout its development been practically free from interference by man or his domestic animals.

Mention may be made of the following insects which were among those listed in the reserve: *Velia caprai*, *Gerris gibbifer*, *Microvelia reticulata*, *Corixa sahlbergi*, *Hydrometra stagnorum*, *Saldula arenicola* and *S. saltatoria* (the last two taken from seepage flowing out from permeable Cretaceous strata overlying impermeable Lias slabs). Mr E. S. Brown comments that the record of the former is probably new for the locality, and is of special interest as this rare Saldid occurs under very similar coastal conditions on cliffs at Highcliffe-on-Sea.

After indulging in a Devonshire cream tea, a short stop was made at Bicton Common where Dr M. J. Delany gave an account of his experiments on the microclimatic conditions beneath *Calluna vulgaris*, the habitat of the Thysanuran *Dilta littoralis*. The higher parts of the heath are occupied by a community of *Calluna* and *Ulex gallii*, often of a somewhat damp facies with much *Molinia coerulea* and *Erica tetralix*, alternating with areas dominated by *Agrostis setacea* and *Ulex gallii*. In the wetter central parts *Schoenus nigricans* and tussocky *Molinia* are prominent and *Rhynchospora fusca* was seen. *Corixa sahlbergi* and *Gerris gibbifera* were again taken, the latter—as at Yarner Wood—heavily infested with the mite *Limnochares aquatica*.

On Monday, 15 July, the Society went to the Plymouth Marine Biological Laboratory, where Dr D. P. Wilson welcomed us on behalf of the Director. We were plied with refreshments in a large marquee, where we had the chance to meet again the many ecologists on the staff.

The party was subdivided into small groups and guided round the laboratory to see a wide variety of activities concerned with the study of marine organisms.

The redesigned storage tanks for sea water now provide wonderfully translucent water for the exhibition tanks, where a good range of the larger fishes, crustacea and anemones are on public view. The research exhibits were of bewildering variety. Not only were many of the common shore forms shown to us, but there were living deep-sea corals and fantastic abyssal fishes and squids in pickle, as well as the apparatus with which they were captured. Dr D. P. Wilson showed some of his exquisite photographs of marine organisms, both large and microscopic, and at the other end of the scale were the electron photomicrographs of marine phytoplankton shown by Dr M. Parke.

The impressive new library wing was much admired and some zoologists eagerly took the opportunity of acquiring copies of the newly revised Plymouth Marine Fauna. During the afternoon, Dr G. M. Spooner led a party of botanists to see some of the natives and naturalized flora of Plymouth Hoe, among which were seen such interesting species as *Carduus pycnocephalus*, *Eryngium campestre*, *Lobularia maritima*, *Senecio cineraria*, *S. vulgaris* ssp. *macrocarpa*, *Silene angustifolia* and *Tragopogon pratensis* ssp. *pratensis*. On the laboratory lawn *Poa bulbosa* was to be seen.

The weather was kind and the liquid supplementation to our luncheon sandwiches (kindly organized by Dr Parke) was greatly appreciated by all. We came away feeling that the day had been very well spent, but that it had been all too short for us to do justice to the place.

The Society is most grateful to the University of Exeter for inviting us to hold our meetings in the University buildings, and to Professor J. Caldwell and Professor L. A.

Harvey for so kindly offering us the hospitality of their departments. The warmest thanks of all who attended go to Mr T. J. Wallace who, as Local Secretary, was so largely responsible for the success of the meeting, and to his colleagues on the staffs of the Botany and Zoology Departments who, with members of the Nature Conservancy, shared with him the conducting of the excursions.

C. H. G.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDED 31 DECEMBER 1957

1956	*Income*	£ s. d.	£ s. d.
	Subscriptions receivable:		
	(Including Arrears and *less* Payments in Advance):		
635	Members taking *Journal of Ecology* only	651 3 10	
331	Members taking *Journal of Animal Ecology* only	371 5 5	
390	Members taking both Journals ...	424 9 6	
6	Associates	4 2 6	
	Reserved for 1957, second part of *Journal of Animal Ecology*	203 10 0	
1362		1654 11 3	
	Less Reserve carried forward to 1958 (for second part of *Journal of Animal Ecology*)	219 0 0	
203			1435 11 3
1159			
	Interest received:		
162	Investments	148 0 0	
29	Deposit Account	11 9 6	
72	Post Office Savings Account	37 19 6	
263			197 9 0
	Watson's Catalogue of British Lichens:		
—	Sales		15 0
	Biological Flora of British Isles:		
	Sales	53 14 3	
—	*Less* Costs	46 13 3	
			7 1 0
	Journal of Ecology, Index Volumes 1-20:		
	Sales	2 14 0	
2	*Less* Costs	8 1	
			2 5 11
824	*Net Deficit for the year transferred to Balance Sheet*		5767 10 6
2248			£7410 12 8

1956	*Expenditure*	£ s. d.	£ s. d.
	Working Expenses:		
42	Expenses of Meetings	88 19 6	
15	Clerical Assistance	27 6 0	
18	Audit Fee, etc.	18 7 6	
21	Postages, etc.	27 13 8	
39	Printing and Stationery	20 8 4	
29	Travelling	23 7 0	
6	Addressograph, Stencils, etc.	5 0 6	
1	Telephone	— — —	
2	Bank Charges	10 10	
173			211 13 4
	Grants and Subscriptions:		
	Freshwater Biological Association ...	2 2 0	
	British Committee for International Nature Conservation	2 2 0	
12			4 4 0
	Journal of Ecology:		
1597	Costs *less* Sales		6039 1 8
	Journal of Animal Ecology:		
100	Costs *less* Sales		871 16 11
—	*Loss on Sale of Investments*		283 16 9
	Biological Flora of British Isles:		
366	Cost *less* Sales		— — —
2248			£7410 12 8

	Journal of Ecology:		
	Sales:		
1846	Current Volume 45		3501 10 6
428	Back Volumes and Parts		899 18 6
4	Reprints of Papers		18 6
—	Contributions towards Costs of extra Plates		98 2 0
2278			
1597	*Loss on Journal transferred to Revenue Account*		6039 1 8
3875			£10,539 11 2

	Journal of Ecology:		
	Costs:		
3181	Printing, Paper, Blocks and Binding: Volume 45		6070 12 5
—	Reprinting Volumes 32, 35-38 ...		3107 2 8
457	Publisher's Commission		920 8 4
220	Carriage, etc.		365 16 4
9	Editorial Expenses		26 0 5
8	Miscellaneous Expenses		49 11 0
3875			£10,539 11 2

	Journal of Animal Ecology:					
	Sales:					
—	Volume 25, No. 2			655	13	4
667	Volume 26, No. 1			1006	6	7
706	Back Volumes and Parts			1279	16	11
16	Abstracts			4	16	11
	Loss on Journal transferred to Revenue					
100	*Account*			871	16	11
1489				£3818	10	8

	Journal of Animal Ecology:					
	Costs:					
	Printing, Paper, Blocks and Binding:					
—	Volume 25, No. 2			1263	12	1
1073	,, 26, No. 1			1242	14	10
—	Reprinting Volume 13, Nos. 1 and 2			331	8	7
36	Binding Back Issues			301	10	0
59	Carriage, etc.			169	19	11
286	Publishers' Commission			479	15	1
25	Editorial, and Literature Reference Checking Expenses			24	17	2
10	Miscellaneous Expenses			4	13	0
1489				£3818	10	8

BALANCE SHEET AS AT 31 DECEMBER 1957.

1956	*Assets*	£	s.	d.	£	s.	d.
	Cash at Bank						
	At Westminster Bank Ltd.:						
703	Current Account	712	14	2			
1400	Deposit Account	100	0	0			
					812	14	2
2970	Post Office Savings Bank Account ...				107	13	0
23	Sundry payments in advance:						
	(Meeting expenses)				16	3	10
	Publishers Accounts due:						
	Journal of Animal Ecology 26—No. 1 ...	199	0	8			
	Biological Flora	7	1	0			
2	Index Volume to *Journal of Ecology* ...	2	5	11			
					208	7	7
	Commissioners of Inland Revenue:						
38	Income Tax recoverable				31	17	6
—	Sundry Debtors				20	0	0
	Investments—at cost:						
	£400 of 3½% War Stock	410	1	4			
	£700 of 3% Post Office Savings Bonds 1960/70	700	0	0			
	£300 of 3% Post Office Savings Bonds 1965/75	300	0	0			
	£1000 of 3% Redemption Stock 1986/96	1005	18	6			
	£1500 of 4% Federation of Rhodesia & Nyasaland Stock 1972/74	1519	3	0			
4755					3935	2	10
9891					£5131	18	11

1956	*Liabilities*	£	s.	d.	£	s.	d.
	Members Subscriptions:						
44	Paid in advance for 1958/62				102	0	11
1	Library Fund				1	5	0
	Publishing Accounts owing to:						
	Blackwell Scientific Publications Ltd.:						
2047	*Journal of Ecology*				2984	0	7
	Reserve of Subscriptions for 1957:						
204	(Allocated to second part of *Journal of Animal Ecology*)				219	0	0
	General Revenue Account:						
	Surplus in hand at 31 December 1956	7593	2	11			
7593	*Less* Net Deficit for the year 31 December 1957	5767	10	6			
					1825	12	5
2	Sundry Accounts owing				—	—	—
9891					£5131	18	11

We have examined the Balance Sheet and Income and Expenditure Accounts of the British Ecological Society as at December 31st, 1957, set forth above. We have obtained all the information and explanations we have required, and have verified the investments and Balance at Bank. In our opinion the above Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Society's affairs, according to the best of our information and the explanations given us, and as shown by the books of the Society.

V. S. SUMMERHAYES
C. E. HUBBARD } *Hon. Treasurers*

RYLAND CLIFT & MORRISON, *Incorporated Accountants*
10 Eccleston Place, Westminster, S.W.1. 19 *February* 1958

NOTICE TO CONTRIBUTORS

Contributors are asked to study these notes with care in order to save themselves and the editor unnecessary work in the revision of manuscripts.

1. All correspondence should be addressed : **The Editor, Journal of Animal Ecology, The Ferry House, Ambleside, Westmorland.**

2. TEXT. MSS should be typed double-spaced on one side of the paper, leaving top and left-hand margins at least an inch wide. Latin names of genera and species, **but nothing else,** should be underlined. Dates should be in the form '1 Jan. 1956, 25 June' etc., not 'Jan. 1st., or with the month indicated by a figure. Text-figures are to be referred to as 'Fig. 1', etc. In the use of symbols, signs and abbreviations *British Standard 1991 : Part I : 1954* should be followed, including the omission of all unnecessary full stops.

The *Journal*'s conventions regarding cross-headings should be followed, but they should not to be used too freely, **nor should headings be underlined.** Only long papers need include a table of contents. The Royal Society's *General notes on the preparation of scientific papers* should be followed on points not mentioned here.

3. LATIN NAMES. Excepting those of British vertebrates, all Latin specific names should be followed by the authority when the name is first mentioned in the text or tables. Names must be verified either from a standard list such as Kloet and Hincks's *Check-List of British Insects* or by submitting the final MS to the experts who have supplied the identifications.

4. REFERENCES should be listed in alphabetical order at the end of the paper in the form:

Vevers, H. G. & Fisher, J. (1938). The 1938 census of gannets (*Sula bassana*) on Ailsa Craig. *J. Anim. Ecol.* **7,** 303-4.

Titles of journals should be abbreviated according to the *World List of Scientific Periodicals*, except that the English usage of capitals for adjectives should be followed. Any reference not personally seen should be marked with an asterisk. **Nothing** except Latin names of genera and species should be underlined, nor should titles of papers or books be put in inverted commas.

5. TABLES should be set out on separate sheets and numbered in arabic numerals. So far as possible sufficient description should be included in the headings to make tables self-explanatory. The layout of tables should be kept as simple as possible; they are not printed 'boxed'.

6. TEXT-FIGURES. Drawings should be in jet-black indian ink, preferably on Bristol board. Shading must consist of lines or dots, not of half-tone washes. If the addition of mechanical stippling or hatching is required the area should be indicated by hatching lightly in blue pencil. Drawings should be arranged or grouped so that after suitable reduction a figure about 5 in. wide results. Graphs should be drawn on paper ruled in blue or faint grey; axes and graduation marks must be drawn in indian ink. All lettering, numerals and arrows should be shown lightly in pencil for insertion in uniform style by the blockmaker. The author's name and the number of the figure should be written on the back of each. Legends for figures should be collected together at the end of the MS.

7. PLATES. Photographs will only be used to illustrate important points which cannot conveniently be shown in any other way. Unmounted, glossy, half-plate prints showing good detail and moderate, but not excessive, contrast, are required. They should be numbered separately from text-figures, and each print should bear on its back the number and the author's name.

8. PROOFS. Page-proofs only will be sent. They should be returned with the least possible delay, and the minimum of essential correction should be made. Authors are requested to pay particular attention to the checking of numerical matter, mathematical formulae, tables and lists of names.

9. OFFPRINTS. Authors are supplied with 50 offprints gratis. Additional copies may be purchased if ordered when the proofs are returned. Contributors from abroad should order when sending their MSS. Offprints are sent out about a month after publication.